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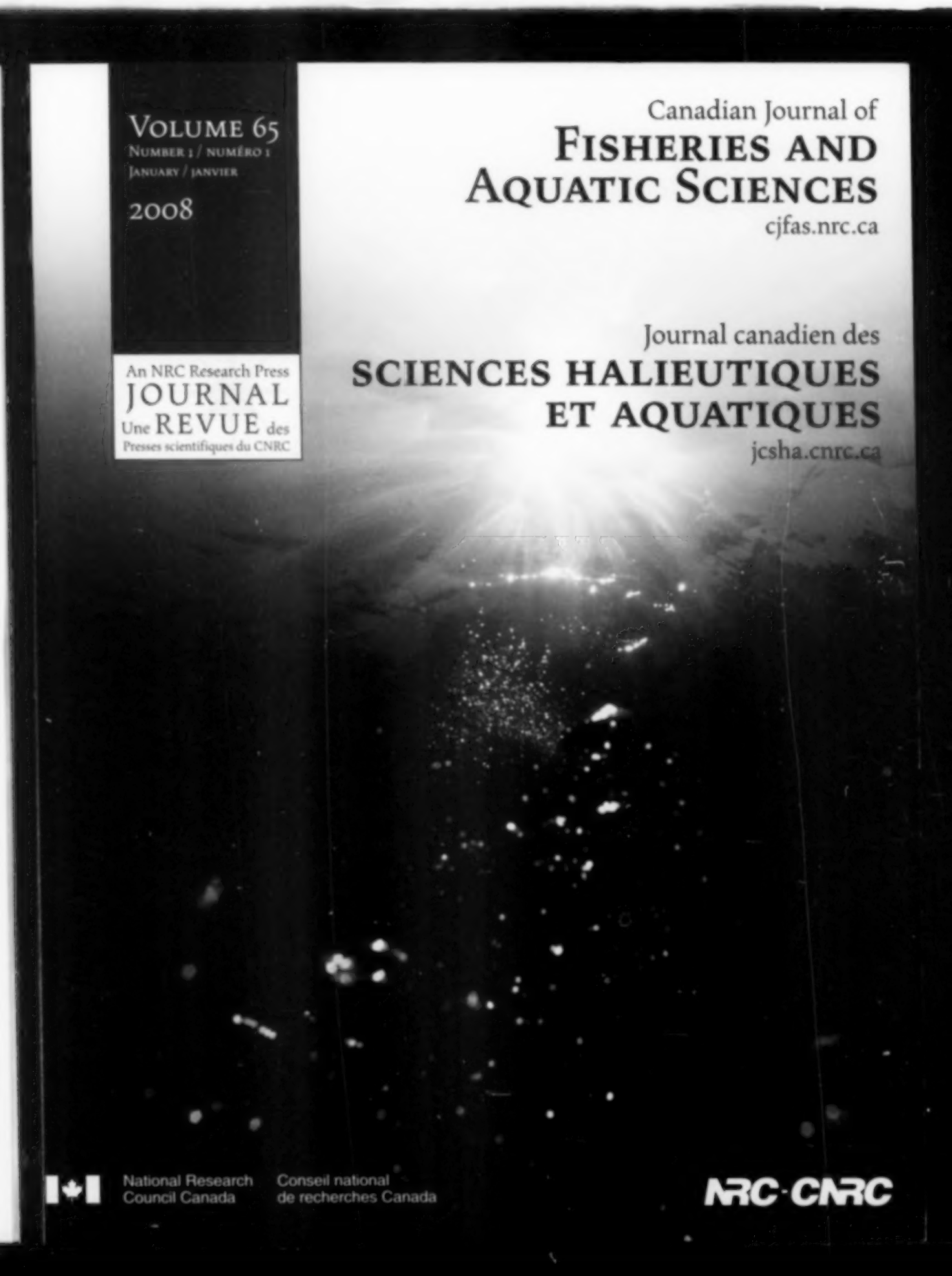

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The *Canadian Journal of Fisheries and Aquatic Sciences*, previously published as *Contributions to Canadian Biology* 1901–1925, *Contributions to Canadian Biology and Fisheries* 1926–1934, *Journal of the Biological Board of Canada* 1934–1937, and *Journal of the Fisheries Research Board of Canada* 1938–1979, is issued monthly to form annual volumes of 12 numbers plus supplements.

Editorial policy. The Journal publishes original research articles, perspectives (syntheses, critiques, reevaluations), discussions (comment and reply), and rapid communications. Manuscripts may concern cells, organisms, populations, communities, ecosystems, or processes that affect aquatic systems. They may cover a range of disciplines including biology and ecology of marine and freshwater organisms, limnology, oceanography, physiology, toxicology, genetics, economics, disease, and management. Preference will be given to manuscripts that emphasize understanding of observed phenomena and interpretation of experimental results. The Journal encourages papers that lead from clearly stated purpose or rationale and from testable hypotheses, concepts, or questions to identifiable conclusions or syntheses. Such papers may amplify, modify, question, or redirect accumulated knowledge embodied in contemporary perceptions of a particular state of aquatic sciences. The Journal discourages papers that are essentially descriptive, except in emerging disciplines; have only site-specific or local applications (a certain year, place, taxon, chemical compound, etc.); only confirm previously established principles; or apply standard techniques without breaking new methodological ground.

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Cameron Macdonald
Director
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Ce projet n'aurait pas été possible sans la contribution des sociétés et des communautés scientifiques de chacune des revues. Les Presses scientifiques du CNRC remercient sincèrement toutes les personnes ayant participé à l'effort.

Les bibliothèques de recherche du milieu universitaire ont aussi contribué à ce projet en se procurant un accès aux revues. Contrairement à certains éditeurs, les Presses scientifiques offrent un accès permanent aux archives, sans frais d'administration annuels. Pour plus de détails, consultez la publicité dans ce numéro.

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Cameron Macdonald
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Cette revue mensuelle publie des articles contribuant, via l'apport de nouvelles connaissances d'importance ou d'une compréhension approfondie, à l'enrichissement des sciences halieutiques et aquatiques. Ceux-ci traitent de disciplines variées, y compris la biologie et l'écologie des organismes d'eau douce et d'eau salée, la limnologie, l'océanographie, la physiologie, la toxicologie, la génétique, l'économie, les maladies et la gestion. Elle est l'une des 16 revues des Presses scientifiques du CNRC, la maison d'édition scientifique la plus importante au Canada.

Il s'agit d'une initiative en recouvrement de coûts. Ainsi, nous aimerions élargir l'accès à nos collections en offrant les archives tout à fait gratuitement vers la fin de 2009, une fois les coûts entièrement recouvrés. Nous espérons que le milieu STM et les bibliothèques appuieront notre objectif et contribueront au succès de cette initiative.

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EDITORIAL / ÉDITORIAL

I am pleased to serve as the new Editor for the *Canadian Journal of Fisheries and Aquatic Sciences*. During this past summer, we began a transition at the Journal from the team led by Moira Ferguson to the present one. Assuming this role is a pleasure given the leadership shown by Moira, Jeff Hutchings, Pierre Pépin, and Gary Sprules, each of whom provided exceptional amounts of time and effort in maintaining, guiding, and enhancing the scientific quality for which the Journal is known. The Board of Associate Editors comprises leading researchers, and I have found it rewarding to discuss ideas with them. The strong support and time that they volunteer speaks to the reputation of the Journal. For most of us, from author to reviewer to Associate Editor, our most direct interaction with the Journal is via Holly Foster. Holly has been with the Journal for many years and shall continue in her role of managing the editorial process for CJFAS and its contributors. Holly's care, attention, and occasional prodding serve to keep the manuscripts moving through the system and provide a friendly "face" for the Journal. I am pleased to have Rolf Vinebrooke serving as Vice-Editor for CJFAS, and Rolf is involved in overseeing many manuscripts as well. I wish to thank all involved for their past efforts and look forward to continuing with those interactions and developing relationships with new members of our Board of Associate Editors.

The general editorial policy of the Journal remains the same as it has been for the past 25 years (Can. J. Fish. Aquat. Sci. **40**: 1–2). This is identified on the Journal's website, in our Instructions to Authors, and on the inside cover of each issue. We strive to maintain broad coverage of research across the aquatic sciences, both freshwater and marine, and in fisheries, both classical fisheries and general fish biology. We are interested in high-quality submissions that significantly advance our knowledge of the study system. These types of studies will be favoured over submissions that are essentially descriptive, confirmatory in nature, or those that are simply providing applications of existing ideas and approaches to different locations and systems. Studies that will encompass interest across fields and those integrating and synthesizing ideas within their discipline or across disciplines are encouraged. While the word "Canadian" appears in our title and speaks to our heritage from the Journal's inception in 1901, the majority of our contributions are international, and we welcome submissions from around the world.

The criteria for consideration remain those identified previously:

There are essentially four criteria for the Journal to evaluate in any contribution:

(1) that the subject/discipline itself falls within the Journal's scope;
(2) that the emphasis is on concepts, interpretation, and understanding, rather than description;
(3) that the manuscript constitutes an "original" contribution to its discipline or beyond; and
(4) that the scientific merits of the contribution warrant publication. [Can. J. Fish. Aquat. Sci. **55**: iii–iv]

C'est avec plaisir que j'ai accepté le poste de directeur scientifique du *Journal canadien des sciences halieutiques et aquatiques*. À l'été dernier, nous avons amorcé la transition de l'équipe de rédaction dirigée par Moira Ferguson à l'équipe actuelle. Mon nouveau rôle a été grandement facilité par les talents d'organisateurs de Moira, de Jeff Hutchings, de Pierre Pépin et de Gary Sprules qui ont consacré tant de temps et d'efforts pour conserver, diriger et améliorer la qualité scientifique qui fait la réputation de la revue. J'ai aussi eu l'avantage de pouvoir échanger des idées avec le Comité des directeurs scientifiques associés, tous des spécialistes reconnus. Leur appui indéfectible et le temps qu'ils acceptent de consacrer gracieusement à la revue reflètent bien sa réputation enviable. Pour la plupart d'entre nous, auteurs, réviseurs, directeurs associés, l'interaction avec la revue se fait principalement par l'intermédiaire de Holly Foster. Holly travaille pour la revue depuis de nombreuses années et elle continuera à gérer les processus d'édition et à assurer la coordination des divers collaborateurs. Ses soins, son attention et, à l'occasion, ses rappels à l'ordre, ont pour but d'accélérer le passage des manuscrits dans le système, tout en donnant un visage « humain » à la revue. Je suis heureux que Rolf Vinebrooke ait accepté d'être vice-directeur scientifique de la revue, sans abandonner l'évaluation des manuscrits. Je veux remercier tous ceux qui se sont impliqués jusqu'à ce jour et j'anticipe le plaisir de maintenir avec eux de bonnes interactions ainsi que d'établir de bonnes relations avec les nouveaux membres du Comité des directeurs associés.

La politique éditoriale générale de la revue reste la même depuis 25 ans (J. can. sci. halieutiques aquat. **40**: 1–2). Celle-ci est décrite sur le site Web de la revue, dans les recommandations aux auteurs et sur les pages intérieures de couverture de chaque numéro. Nous essayons de couvrir de façon large toutes les sciences aquatiques, tant en mer qu'en eau douce, ainsi que les sciences halieutiques, autant la pêche classique que la biologie générale des poissons. Nous recherchons des manuscrits de haute qualité qui font progresser de façon significative les connaissances dans ces domaines. Ces types de travaux seront préférés à ceux qui sont surtout descriptifs, qui confirment des études antérieures ou qui suggèrent des applications inédites d'idées ou de méthodologies connues à des sites ou des systèmes nouveaux. Les études qui sont d'intérêt pour plusieurs disciplines ou qui font la synthèse et l'intégration d'idées dans leur propre discipline ou dans plusieurs matières sont particulièrement bienvenues. Quoique l'épithète « canadien » fasse partie du nom de la revue et témoigne de son héritage depuis sa fondation en 1901, la plupart de nos collaborateurs proviennent de la communauté scientifique à l'étranger et nous accueillons des manuscrits de tous les pays.

Les critères qui assurent qu'un manuscrit sera examiné sont ceux qui ont été identifiés précédemment :

Les articles soumis au Journal sont évalués à la lumière de quatre critères principaux :

(1) le sujet/la discipline doit cadrer avec l'orientation du Journal;
(2) on doit s'y attarder aux concepts, à l'interpration et à la compréhension plutôt que la simple description;
(3) l'article doit constituer une contribution « originale » dans sa discipline ou frayer la voie à de nouvelles découvertes;
(4) la valeur scientifique de l'article doit justifier sa publication. [J. can. sci. halieut. aquat. **55**: iii–iv]

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Given the large number of submissions and the fact that we are unable to publish all that we receive, manuscripts that do not meet these criteria may be returned to the authors without review. Such an outcome should not be viewed as being negative, but will hopefully allow the authors to better target their work to a more suitable journal and reduce the time to its publication elsewhere.

Although the Journal remains largely unchanged in its direction, we plan to introduce some new features during the coming year. These additions will allow us to better target particular areas of research that may not be as well represented as desired and to help stimulate some active discussion regarding our research. While we will introduce these features, the primary goal of the *Canadian Journal of Fisheries and Aquatic Sciences* will remain the broad coverage of high-quality papers advancing our knowledge and understanding.

I look forward to working with you over the coming years. I welcome your ideas and constructive criticisms in furthering our goals.

Donald A. Jackson
Editor

Étant donné que de nombreux manuscrits nous sont soumis et qu'il nous est impossible de les publier tous, ceux qui ne satisferont pas aux critères susmentionnés pourront être retournés aux auteurs sans avoir été soumis à nos réviseurs. Un tel processus ne doit pas être perçu négativement; il vise à encourager les auteurs à acheminer leur manuscrit vers une revue plus appropriée et à en accélérer ainsi la publication.

Bien que l'orientation de la revue demeure principalement inchangée, nous pensons faire quelques innovations au cours de l'année qui vient. Celles-ci nous permettront de mieux cibler des domaines de recherche qui ne sont pas aussi bien représentés qu'on le voudrait et chercheront à stimuler des discussions animées sur nos recherches. Malgré ces innovations, la *Revue canadienne des sciences halieutiques et aquatiques* continuera de poursuivre son objectif principal qui est de présenter un vaste éventail d'articles de grande qualité qui font avancer connaissances et compréhension dans notre discipline.

C'est avec confiance que j'envisage de collaborer avec vous au cours des prochaines années. Je demeure ouvert à la soumission de vos idées et critiques constructives dans la poursuite de la réalisation de nos objectifs.

Donald A. Jackson
Directeur scientifique

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TRIBUTE

Ransom Aldrich Myers (1952–2007): In memoriam

Jeffrey A. Hutchings

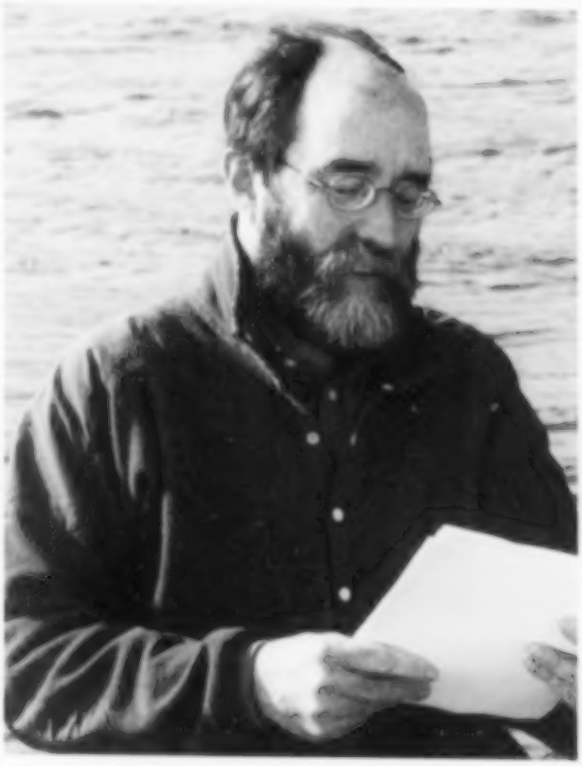
Ransom Aldrich Myers (Ram) was a mathematically gifted, intellectually pugnacious, and passionately humane scientist committed to the unconstrained communication of science to decision makers and to society (Fig. 1). He died 27 March 2007 in Halifax, Nova Scotia, Canada, 4 months after being diagnosed with inoperable brain cancer. He was 54 years old and in the prime of his scientific career.

Beginnings

The son of a cotton plantation owner in the southern United States, Ram (Randy to his parents and siblings) was born on Friday, the 13th of June, 1952, in the rural community of Lula, Mississippi. After graduating with a B.A. in Physics from Rice University in Houston in 1974, Ram spent 2 years working for Schlumberger Overseas S.A. in the oil fields of Kuwait. He then spent his 23rd year travelling throughout Africa before embarking across the Atlantic to the Caribbean on an 8.5 m sailboat. In 1977, rather than disappointing his father (whose ancestors included Confederate soldiers) by attending a university in the northern "Yankee" states, Ram left the United States for Canada, a country he first visited as a 13-year-old when his cousin took him there on a canoe trip to Ontario's Algonquin Park. Having enrolled in postgraduate studies at Dalhousie University under the supervision of Roger Doyle, Ram defended his M.Sc. in Mathematics on 6 October 1980 before defending his doctorate in Biology 3 years later (20 August 1983).

One would have been hard pressed to predict most of Ram's future research endeavours based on his postgraduate thesis topics. In his M.Sc. thesis (dedicated simply "To my mother"; she had died 2 years before his thesis defence), he presented a model for the evolution of dispersal, based on a nonlinear, stochastic system of difference equations. His primary conclusion was that "the ESS [Evolutionarily Stable Strategy] dispersal distribution is independent of dominance, model assumptions of haploidy or diploidy, maternal or individual genotypic control of dispersal, and the timing of mating" (Myers 1981). The overall objective of his doctoral thesis (Myers 1983) was to use optimization and inverse optimization theory to study the evolution of life histories, focussing in particular on the evolutionary stability of postmaturation growth, the degree to which reproduction–mortality trade-offs could be used to estimate natural mortality rates, and the adaptive basis for empirical patterns of covariation between growth rate and size at maturity.

Fig. 1. Ransom Aldrich Myers (Ram) photographed near Halifax, Nova Scotia (February 2004).



Prior to defending his doctoral thesis, Ram accepted a position as research scientist in the Department of Fisheries and Oceans (DFO) in St. John's, Newfoundland, where he undertook work on Atlantic salmon, *Salmo salar*. At the time, I was an M.Sc. student, nearing the end of one of two 6-month field seasons. I had collected reams of life history

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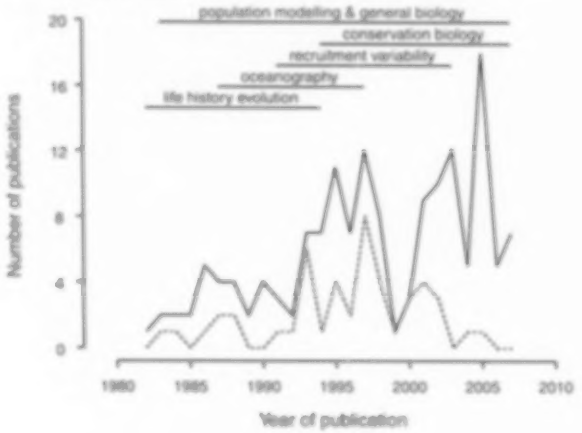
data on two migratory variants of Atlantic salmon in Terra Nova National Park, northeastern Newfoundland, when John Gibson, a DFO scientist of British descent, remarked, "Jeff, we've just hired a new scientist — Ransom Myers — and he's very interested in salmon. I told him about your work. You really ought to meet this chap." It was the first and only time I heard Ram referred to as a "chap" — many other things mind you, but chap was never amongst them. Although we met briefly at a DFO seminar shortly thereafter in October 1983, it was not until April 1984, when I was a financially challenged postgraduate and Ram was a financially flush government scientist, that he hired me as a research associate.

I am not sure whether Ram was prepared for Newfoundland, but I think it is fair to say that Newfoundland was not entirely prepared for Ram. At 31 years, he possessed a massive head of dark-brown hair and a long, flowing beard. When standing on a rock, overlooking the ocean, in a Newfoundland "breeze", the beard did lend Ram a certain physical presence not unlike that of Thor, the Norwegian god of thunder. It was a prescient characterization fitting for a man who would slay many a sacred cow with his question-laden, data-infused hammer.

However, looking god-*like* in a William Blake or Michelangelo sort-of-way was one thing, but it did not come with any divinely bestowed power of flight. We had to drive to work. Every morning, I would pick Ram up at his home, and we would navigate the 5 km or so to DFO on the White Hills in St. John's. I learnt very quickly that Ram was a creature of habit. While I parked at the curb, he would scramble down the steps with a backpack full of books and papers in one hand and a steaming mug of coffee in the other. Riding shotgun, sans lid, only a portion of this coffee ever made it down Ram's throat. As Ram might have put it, the probability of the coffee finding its way to the floor, seat, or dash of the car was nontrivial. On other occasions, reckoning that a half mug of coffee would not quite do it, Ram decided that a full breakfast was in order. With his backpack over a shoulder, he would gingerly make his way to the car, nursing the ubiquitous coffee in one hand and balancing a bowl of cereal, milk, and spoon in the other. Then we would drive off, Ram simultaneously gesticulating, eating, and talking, while I minded the coffee.

Unsurprisingly, given the topics of his postgraduate thesis research, Ram was adamant that fundamentally important questions in biology could not be addressed without a sound knowledge of ecology, evolutionary biology, and quantitative genetics. He argued this point repeatedly (among others) during Ecology and Evolution Discussion Group meetings held weekly in the Biology Department at Memorial University of Newfoundland. The verbal jousting that took place between Ram and people such as Doug Morris and Jake Rice, neither of whom could be described as shrinking violets, were legendary both for the degree of uninhibited enthusiasm they exuded and for the unparalleled influence their interactions had on some of us during our formative postgraduate years. It was Ram who, all before 1987, introduced me to life history evolution, additive genetic variance, epistasis, John Maynard Smith, ESSs, maximum likelihood, APL (A Programming Language, a computer program for which the sole username at DFO was "droff", after Derek Roff), John Thorpe, threshold traits, the quantitative genetics of liability, Sewall Wright, and Ronald Fisher.

Fig. 2. Number of research contributions (including anonymously peer-reviewed book chapters and papers in the primary scientific literature, but excluding letters, consultant reports, and government research documents and working papers) authored or co-authored by Ram Myers from 1982 to 2007. Solid line represents the total number of contributions; the broken line represents those published in the *Canadian Journal of Fisheries and Aquatic Sciences*. The labelled horizontal bars identify the range in publication year for six research themes.



One of my most cherished "Ram-isms" was his response to my scepticism of the utility of, and logical basis for, distinguishing between *r*- and *K*-selection (a scepticism I firmly embrace today). Ram's simple response, written in his own uniquely expressive hand, was "r-K-ic". Among the myriad interactions we were to share over the coming years, none, but for these four letters, captured quite so well the succinctness, wit, clarity, and mischievousness that Ram was always capable of.

Research contributions and collaborations

Ram's breadth of interest in the arts (he read all manner of nonfiction voraciously, loved live theatre, and thoroughly enjoyed opera) was mirrored by the diversity of the science he undertook. At the time of writing (December 2007), Ram had co-authored 153 research contributions (including anonymously peer-reviewed book chapters and papers in the primary scientific literature, but excluding letters, consultant reports, and government research documents and working papers). His primary research outlet was the *Canadian Journal of Fisheries and Aquatic Sciences*, the journal in which almost half (46%) of his 98 papers through to 2002 were published (47 of 141 papers overall) (Fig. 2). Among these was his first scientific paper, which explored ways of estimating natural mortality and associated trade-offs from fish life history data (Myers and Doyle 1983) and his first sole-authored paper, which documented a survival cost of reproduction in mature male Atlantic salmon parr (Myers 1984). He also co-authored nine publications in *Science* and three in *Nature* (including a Reply).

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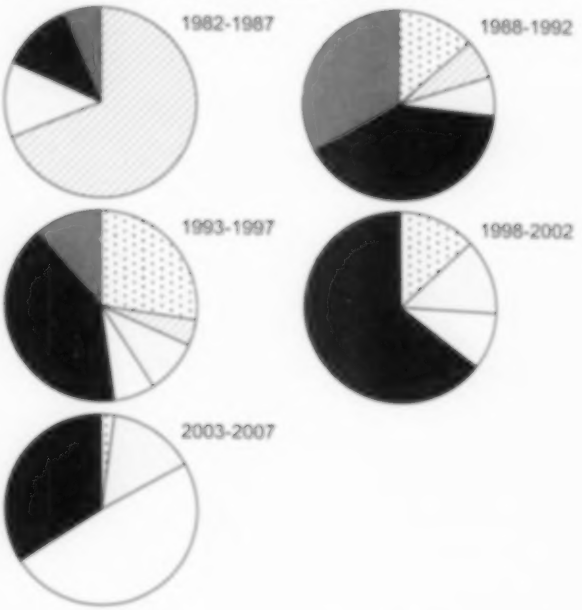
Fig. 3. Proportional representation of research contributions by Ram Myers for each of six research themes: life history evolution (hatched area), oceanography (dark grey), recruitment variability (stippled area), conservation biology (open), population modelling (solid), and general biology (light grey).



Ram worked very closely with others, successfully combining his modelling and mathematical skills with the varied strengths of his collaborators, a group that included fisheries scientists, statisticians, stock assessment modellers, conservation biologists, oceanographers, field biologists, evolutionary ecologists, natural historians, and legal scholars. Numerically, the most prominent of his collaborators were Nick Barrowman (n = 18 publications), Jeff Hutchings (n = 16), Gordon Mertz (n = 16), Mike James (n = 10), and Boris Worm (n = 9). Among others who co-authored five or more papers with Ram were Noel Cadigan, Ken Drinkwater, Jamie Gibson, Mike Hammill, Ian Jonsen, Dan Kehler, Andy Rosenberg, and Gary Stenson. Additional collaborators, each of whom co-authored three of Ram's dual-authored contributions, included Bill Montevecchi, Pierre Pepin, Jeff Runge, and Peter Ward. Even if not identified explicitly, the contributions of these individuals and many others are interwoven within the fabric of the corpus of Ram's research.

Research career

Newfoundland

Upon arrival at DFO, Ram learned of data on salmon parr collected between 1956 and 1963 in Little Codroy River, Newfoundland. Quickly grasping the uniqueness of this data set, he immediately set about estimating the heightened mortality experienced by mature male parr relative to immature males and the loss of anadromous salmon productivity that would ensue (Myers 1984). These analyses comprised part of his work on life history evolution, one of six research themes in which I have attempted to categorize his research contributions (Fig. 3). Predicated by his doctoral thesis research (Myers 1983), Ram's keen interest in how fitness trade-offs influence life history evolution led to a series of papers published in the mid-1980s on alternative reproductive tactics in male Atlantic salmon (Fig. 4). Among his nine co-authored papers that have been cited more than 100 times (hereafter, his highly cited papers), the earliest was a product of this life history research and represented one of the first attempts to use genetic markers to estimate fertilization success in fishes (Hutchings and Myers 1988).

Fig. 4. Photograph of Ram standing next to the Department of Fisheries and Oceans' experimental stream channel at Noel Paul's Brook, a tributary of Exploits River, Newfoundland, where he and I undertook experimental work on Atlantic salmon (October 1984).

In 1989, Ram became part of a small group of modellers and statisticians at DFO that comprised the Resource Assessment and Survey Methodology Centre of Disciplinary Expertise (RASM CODE), under the direction of John Hoenig. This section was intended to serve as a national resource for other DFO research scientists. One consequence of this shift in Ram's responsibilities was a substantive increase in the proportional representation of papers (1988–1992) on various elements of population modelling (particularly the demography of marine mammals), a research theme that was to remain dominant throughout the remainder of his

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career. It was also during this period that Ram's interest in oceanography was most prominent. His work on environmental correlates of larval and juvenile mortality, for example, contributed to his first two publications on recruitment variability (Myers 1991; Pepin and Myers 1991), a topic he was to explore in increasingly greater detail through the 1990s.

The period 1993–1997 was Ram's most wide ranging in terms of research (Fig. 3). It was also the period during which his interest in recruitment was at its height, as Ram examined how density, life history, and oceanography affected the magnitude and spatial scale of recruitment variability. Four of his highly cited papers were published during this period: one examined the influence of density on juvenile mortality in marine fishes (Myers and Cadigan 1993); one represented the first meta-analysis to test for depensation, or Allee effects, in fish stock–recruitment relationships (Myers et al. 1995); and two pertained to the collapse of marine fishes, particularly Atlantic cod, *Gadus morhua* (Hutchings and Myers 1994; Myers et al. 1997*a*).

It seems reasonable to conclude that the diligence and fervour with which Ram undertook his later work in conservation biology had its genesis during the time between 1993 and 1997 when we (Ram, Nick Barrowman, and myself) undertook our work on the collapse of northern cod. The loss of this once massive fishery had, and continues to have, enormous economic, sociological, and emotional impacts on Newfoundlanders. You could not work at DFO in Newfoundland in the early 1990s (as we three did) and not be cognizant of the obligations that scientists have to society of communicating their research widely, publicly, and honestly.

This perspective was not, however, shared by all. The societal and moral obligation of scientists to communicate the results of their research was being traded off by the desire of some bureaucrats to control the information that flowed from DFO to the public. Bureaucratic impediments to the communication of fisheries science were discussed by Hutchings et al. (1997), who reported that a DFO scientist had received an official reprimand for communicating to the media conclusions consistent with the peer-reviewed scientific literature but inconsistent with the views expostulated by department spokespersons. Ram was the scientist in question (according to a memorandum; footnote 1, Hutchings et al. 1997).

Dalhousie University

It was this reprimand that sealed Ram's future with DFO. From his perspective, he could "put up and shut up", or he could leave. He opted for the latter, attaining the right of freedom of expression that universities offer when he returned to Halifax in 1997 as Dalhousie's inaugural Killam Chair in Ocean Studies. Upon arrival at Dalhousie, Ram and postgraduate Jill Casey completed their work on the extraordinary decline experienced by the barndoor skate, *Dipturus laevis*, one of Canada's larger marine fishes (maximum length of 153 cm), that occurred, as Ram frequently put it, "when no one was looking". Indeed, no one was looking, primarily because the focus was traditionally on temporal trends in species directly targeted by the fishing industry. Consequently, changes in the abundance of those species caught incidentally often went unnoticed. The increased attention to bycatch species by fisheries agencies in the early 2000s can be attributed to a considerable degree to the attention generated by Casey and Myers' (1998) highly cited paper in *Science*.

Following intellectually in the footsteps of fisheries scientists Bill Ricker and Ray Beverton and pioneer life history modeller Lamont Cole, it was Ram's primary assertion that the maximum rate of population growth was the single most important parameter required to fully understand the factors that affect the ability of fish populations to sustain exploitation, to resist decline in the face of unpredictable environmental change, and to recover following collapse. It was this parameter (r_{max}) that represented the intellectual and empirical anchor that grounded much of Ram's research, be it the life histories of zooplankton, alternative reproductive behaviours in Atlantic salmon, the relationship between parental and offspring abundance in harvested populations, or the factors that affect the collapse, recovery, and extinction risk of marine fishes.

Two influential examples of Ram's research on maximum population growth were published between 1997 and 1999. Myers et al. (1997*b*) introduced methods to estimate r_{max} from stock–recruit data, applying it here to multiple stocks of Atlantic cod and making explicit the link that exists between r_{max} and recovery. Based on an analysis of more than 700 spawner–recruit relationships, Myers et al. (1999; one of the nine highly cited papers) concluded that maximum annual reproductive rate is relatively constant across a broad range of fish species. Ram declared this result to be a "very important finding" (Myers et al. 1999). A touch of arrogance, to be sure, but on this occasion, as on many others, he was right.

Following the stock–recruitment database that Nick Barrowman, Jessica Bridson, and he had compiled in the mid-1990s and armed with an extraordinarily acute understanding of analytical modelling techniques, Ram continued his marshalling of massive data sets from around the globe. During a 5-year period beginning in 2003, Ram's research contributions to conservation biology reached a pinnacle. Concomitant with a highly cited paper in *Science* on the decline of pelagic sharks in the Northwest Atlantic (Baum et al. 2003), a publication that was a part of Julia Baum's M.Sc. research, Ram and postdoctoral researcher Boris Worm took on the task of estimating the magnitude of the post-1950s decline experienced by large, predatory fishes targeted by industrialized fishing, species such as tunas and billfishes. The authors' conclusion that the global ocean has lost more than 90% of large, predatory fishes attracted an unprecedented amount of attention for a publication in marine conservation biology. The paper by Myers and Worm (2003), published in *Nature*, is the most referenced of Ram's research contributions at present and, having been cited more than 330 times to date, will almost certainly remain so.

It is prudent to note, however, that this recent work has not been without criticism (e.g., Walters 2003; Hampton et al. 2005; Polacheck 2006). In this vein, Ram has been described as one of those responsible for a rift that currently exists between some fisheries scientists who perceive marine fish population declines to have been unduly exaggerated and others who consider it important that studies of marine biodiversity be integrated with studies of fisheries science (Pauly 2007). This is a characterization with which Ram

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Fig. 5. Photograph of George Lilly (left), Ram (centre), and me in my office at the Department of Fisheries and Oceans, White Hills, St. John's, Newfoundland, on the occasion of our Wilfred Templeman Publication Award (December 1993).

would have agreed, finding solace in Winston Churchill's assertion, "You have enemies? Good. That means you've stood up for something, sometime in your life." The last decade has demonstrated the utility of integrating studies of fields typically associated with conservation biology (e.g., ecology, biodiversity, evolution, genetics) with studies typically associated with fisheries science (e.g., temporal changes in fishing mortality, recruitment variability, stock structure). Pauly (2007) coined this field "fisheries conservation biology", identifying Ram as one of its founders.

The paper by Myers and Worm (2003) succeeded in bringing an extraordinary amount of attention to the plight of the world's oceans and to declines in marine fish biodiversity. Among other things, it provided Ram with opportunities to communicate directly with decision-makers and politicians; he served as a witness at hearings of the Canadian House of Commons Standing Committee on Fisheries and Oceans (2003, 2005) and at two US Senate Committee hearings on overfishing (2003). In October 2005, *Fortune* magazine named Ram one of the "Ten to Watch" (i.e., individuals whose work *Fortune* believes will have lasting influence), citing his work on the decline of large predatory fishes. Recognition of Ram's research excellence over the years came in a variety of other forms. Among his awards were the 1993 Wilfred Templeman Award (shared with George Lilly and myself; Fig. 5), a 1996 Visiting Fellowship to Imperial College at Silwood Park (UK), the inaugural Killam Chair in Ocean Studies at Dalhousie University (1997), Memorial University of Newfoundland's Great Auk Lectureship (1999), and the Blue Ocean Society for Marine Conservation Science Award (2004). He also served as Director of the Sloan Foundation's Future of Marine Animal Populations project, member of the World Conservation Union (IUCN) Shark Specialist Group, editor for *Ecology Letters*, and member of science advisory boards for Sierra Club of Canada and *Oceana* (Washington, D.C.).

L'envoi

When Ram died, the first thing I thought about were those breakfasts in my car. I never did say anything to him about the mugs, bowls, and spoons that would be left under the passenger seat, often for several days. The fact that he saw nothing untoward in using my car as a café was, in an odd sort of way, touching. His behaviour in general was not what I was used to, but I was drawn to him nonetheless.

When he did not feel threatened, Ram's demeanour often reflected a child-like sincerity, honesty, and innocence. But it is the innocence of children that makes them vulnerable, and it was this underlying vulnerability, often juxtaposed with uncompromising forthrightness, often juxtaposed with unselfish acts of kindness, that made Ram such a singular individual.

The collapse of Atlantic cod and myriad other marine fishes has occurred on our collective watch in an alarmingly short period of time. The responsibilities we have to those who follow us are non-negotiable. It was acceptance of these societal responsibilities that lay behind the passion and enthusiasm that fuelled Ram's work and the determination with which he communicated the results of his research to society.

There are those who disagreed with Ram, but there are few who would disavow the impact he has had on fisheries science and marine conservation biology. He earned the respect of lawmakers in Canada and the United States. He is lauded for his mentoring of students and for his ability to

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communicate the plight of the world's oceans broadly and meaningfully. Society has benefited from his scientifically driven provocations and his proddings. They have forced us to look very carefully at our oceans, to learn from past mistakes, and to acknowledge that maintaining the health and biodiversity of marine ecosystems is a priority and a fundamental responsibility to future generations. We can neither afford nor have the right to ignore these matters.

Ram Myers was my colleague, my confidante, and my friend, and he is sorely missed. He is survived by his wife, Rita Kindl Myers, and children, Emily, Rosemary, Sophia, Carlo, and Gioia. He also leaves his brother, Abbott Myers, and sisters, Joan Peters and Susan Myers.

References

Baum, J.K., Myers, R.A., Kehler, D.G., Worm, B., Harley, S.J., and Doherty, P.A. 2003. Collapse and conservation of shark populations in the Northwest Atlantic. Science (Washington, D.C.), **299**: 389–392.

Casey, J.M., and Myers, R.A. 1998. Near extinction of a large, widely distributed fish. Science (Washington, D.C.), **281**: 690–692.

Hampton, J., Sibert, J.R., Kleiber, P., Maunder, M.N., and Harley, S.J. 2005. Fisheries: decline of Pacific tuna populations exaggerated? Nature (London), **434**: E1–E2.

Hutchings, J.A., and Myers, R.A. 1988. Mating success of alternative maturation phenotypes in male Atlantic salmon, *Salmo salar*. Oecologia, **75**: 169–174.

Hutchings, J.A., and Myers, R.A. 1994. What can be learned from the collapse of a renewable resource? Atlantic cod, *Gadus morhua*, of Newfoundland and Labrador. Can. J. Fish. Aquat. Sci. **51**: 2126–2146.

Hutchings, J.A., Walters, C., and Haedrich, R.L. 1997. Is scientific inquiry incompatible with government information control? Can. J. Fish. Aquat. Sci. **54**: 1198–1210.

Myers, R.A. 1981. The evolution of dispersal in a stochastic environment. M.Sc. thesis, Dalhousie University, Halifax, N.S.

Myers, R.A. 1983. The use of inverse optimization in evolutionary biology. Ph.D. thesis, Dalhousie University, Halifax, N.S.

Myers, R.A. 1984. Demographic consequences of precocious maturation of Atlantic salmon (*Salmo salar*). Can. J. Fish. Aquat. Sci. **41**: 1349–1353.

Myers, R.A. 1991. Recruitment variability and range of three fish species. NAFO Sci. Counc. Stud. **16**: 21–24.

Myers, R.A., and Cadigan, N.G. 1993. Density-dependent juvenile mortality in marine demersal fish. Can. J. Fish. Aquat. Sci. **50**: 1576–1590.

Myers, R.A., and Doyle, R.W. 1983. Predicting natural mortality rates and reproduction — mortality trade-offs from fish life history data. Can. J. Fish. Aquat. Sci. **40**: 612–620.

Myers, R.A., and Worm, B. 2003. Rapid worldwide depletion of predatory fish communities. Nature (London), **423**: 280–283.

Myers, R.A., Barrowman, N.J., Hutchings, J.A., and Rosenberg, A.A. 1995. Population dynamics of exploited fish stocks at low population levels. Science (Washington, D.C.), **269**: 1106–1108.

Myers, R.A., Hutchings, J.A., and Barrowman, N.J. 1997*a*. Why do fish stocks collapse? The example of cod in eastern Canada. Ecol. Appl. **7**: 91–106.

Myers, R.A., Mertz, G., and Fowlow, S.P. 1997*b*. Maximum population growth rates and recovery times for Atlantic cod (*Gadus morhua*). Fish. Bull. **95**: 762–772.

Myers, R.A., Bowen, K.G., and Barrowman, N.J. 1999. Maximum reproductive rate of fish at low population sizes. Can. J. Fish. Aquat. Sci. **56**: 2404–2419.

Pauly, D. 2007. Obituary: Ransom Aldrich Myers (1952–2007). Nature (London), **447**: 160.

Pepin, P., and Myers, R.A. 1991. Significance of egg and larval size to recruitment variability of temperate marine fish. Can. J. Fish. Aquat. Sci. **48**: 1820–1828.

Polacheck, T. 2006. Tuna longline catch rates in the Indian Ocean: did industrial fishing result in a 90% rapid decline in the abundance of large predatory species? Marine Policy, **30**: 470–482.

Walters, C.J. 2003. Folly and fantasy in the analysis of spatial catch rate data. Can. J. Fish. Aquat. Sci. **60**: 1433–1436.

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HOMMAGE

Ransom Aldrich Myers (1952–2007) : In memoriam

Jeffrey A. Hutchings

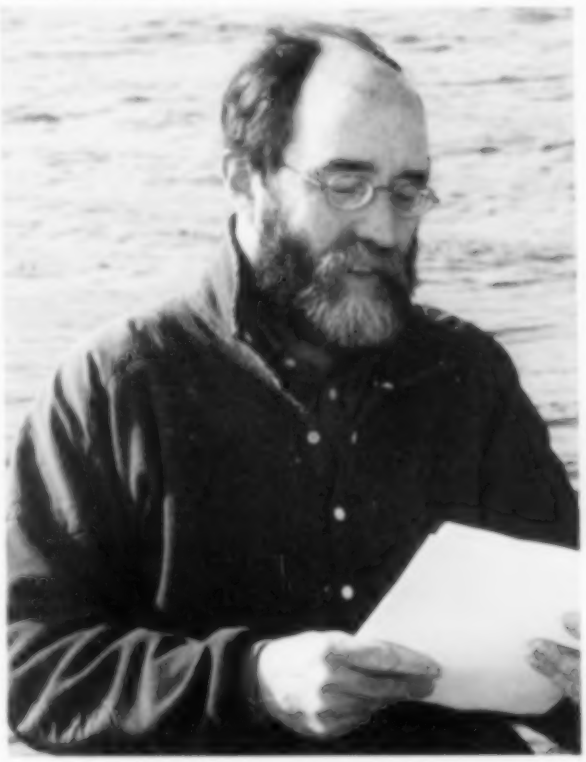
Ransom Aldrich Myers (Ram) était un scientifique doué pour les mathématiques, un intellectuel combatif et un humaniste passionné engagé dans la transmission libre de la recherche scientifique aux décideurs et à la société (fig. 1). Il est décédé le 27 mars 2007 à Halifax (Nouvelle-Écosse), Canada, quatre mois après avoir appris qu'il souffrait d'un cancer inopérable au cerveau. Il avait 54 ans et était au faîte de sa carrière scientifique.

Débuts

Le fils d'un propriétaire de plantation de coton du sud des États-Unis, Ram (Randy pour ses parents et sa famille) est né le vendredi 13 juin 1952, dans la commune rurale de Lula, au Mississippi. Après avoir obtenu un B.A. en physique de l'université Rice de Houston en 1974, Ram a travaillé pendant deux ans dans les champs pétrolifères du Kuwait pour Schlumberger Overseas S.A. Il a passé ensuite sa vingt-troisième année à parcourir l'Afrique avant de traverser l'Atlantique sur un voilier de 8,5 m en route vers les Caraïbes. En 1977, pour ne pas déplaire à son père (fier descendant de soldats de l'Armée des États confédérés) en s'inscrivant dans une université des États « yankees » du Nord, Ram a quitté les États-Unis, pour le Canada, un pays qu'il avait découvert à l'âge de 13 ans quand son cousin l'y avait amené pour une excursion en canot au parc Algonquin en Ontario. Inscrit aux études supérieures à l'université Dalhousie sous la direction de Roger Doyle, Ram a soutenu son mémoire de maîtrise en mathématiques le 6 octobre 1980, et sa thèse de doctorat en biologie trois ans plus tard (20 août 1983).

Les sujets de recherche des études supérieures de Ram ne laissaient pas vraiment prévoir les domaines de prédilection de ses recherches futures. Dans son mémoire de maîtrise (dédicacé simplement à sa mère, décédée deux ans avant la défense), il a présenté un modèle de l'évolution de la dispersion basé sur un système stochastique non linéaire d'équations de différence. Sa conclusion principale était que la distribution de la dispersion ESS (stratégie évolutive stable) est indépendante de la dominance, des présuppositions d'haploïdie ou de diploïdie du modèle, des contrôles génotypiques maternels et individuels de la dispersion et du moment de la reproduction (Myers 1981). L'objectif global de sa thèse de doctorat (Myers 1984) était d'utiliser les théories de l'optimisation et de l'optimisation inverse pour étudier l'évolution des cycles biologiques, avec une attention particulière à la stabilité évolutive de la croissance après la maturation, à la mesure dans laquelle les compromis reproduction–mortalité peuvent servir à estimer les taux de mortalité naturelle, ainsi qu'à la base adaptative des patrons

Fig. 1. Ransom Aldrich Myers (Ram) près de Halifax (Nouvelle-Écosse) (février 2004).



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empiriques de covariation entre le taux de croissance et la taille à la maturité.

Avant d'avoir défendu sa thèse de doctorat, Ram a accepté un poste de chercheur au ministère des Pêches et des Océans (MPO) à St. John's (Terre-Neuve), où il a entrepris des travaux sur le saumon atlantique, *Salmo salar*. À cette époque, j'étais étudiant à la maîtrise vers la fin de l'une de mes deux saisons de terrain de six mois. J'avais récolté des masses de données sur les cycles biologiques de deux variantes du saumon atlantique au parc national Terra Nova, dans le nord-est de Terre-Neuve, quand John Gibson, un chercheur du MPO d'origine britannique, m'a informé : « Jeff, nous venons d'engager un nouveau chercheur — Ransom Myers — qui est très intéressé au saumon. Je lui ai parlé de ton travail. Tu devrais vraiment rencontrer ce « type » (« chap »). » C'est la première et la dernière fois que j'entendis Ram qualifié de « type »; bien d'autres épithètes lui ont été attribuées, il est vrai, mais jamais plus celle de « type ». Bien que nous nous soyons rencontrés brièvement à un séminaire du MPO peu après en octobre 1983, ce n'est qu'en avril 1984, alors que j'étais un chercheur diplômé en difficulté financière et Ram un riche chercheur dans un laboratoire gouvernemental, qu'il m'a engagé comme associé de recherche.

Je ne suis pas sûr que Ram était prêt à affronter Terre-Neuve, mais je pense qu'il n'est pas exagéré d'affirmer que Terre-Neuve n'était pas tout à fait prête à affronter Ram. À 31 ans, il possédait une tête massive couronnée de cheveux brun foncé et ornée d'une longue barbe flottante. Debout sur un rocher, le visage tourné vers la mer face à la « brise » terre-neuvienne, Ram avait à cause de sa barbe une prestance qui pouvait rappeler Thor, le dieu norvégien du tonnerre. C'était une excellente image prémonitoire de celui qui allait abattre tant de vaches sacrées avec son marteau de questions et de données.

Il avait beau avoir l'air d'un dieu, un peu à la manière de ceux de William Blake et de Michel-Ange, il n'était pas doué pour autant de la capacité de voler. Nous devions nous rendre au travail en voiture. Chaque matin, j'allais chercher Ram chez lui et nous traversions les quelque 5 km dans les White Hills qui nous séparaient du laboratoire du MPO à St. John's. Je me suis vite rendu compte que Ram était une personne qui avait ses habitudes. Alors que je l'attendais dans la voiture sur le bord de la rue, il déboulait l'escalier avec un sac à dos plein de livres et de dossiers à la main et une tasse de café fumant dans l'autre. Véritable arrosoir, sa tasse découverte ne lui permettait d'avaler qu'une partie de son café. Comme il l'aurait exprimé lui-même, la probabilité que ce café finisse par se répandre sur la moquette, le siège ou le tableau de bord n'était pas négligeable. D'autres jours, ayant décidé qu'une demi-tasse de café ne suffisait pas, il apportait un petit déjeuner complet. Le sac à dos sur l'épaule, il avançait vers l'auto avec précaution avec l'indispensable café à la main, tout en jonglant avec un bol de céréales et de lait et une cuiller. Et nous prenions la route pendant que Ram gesticulait, mangeait et parlait, alors que je m'occupais de son café.

Comme on pouvait s'y attendre dans la continuité des sujets de ses travaux d'études supérieures, Ram insistait sur le fait que les questions d'importance fondamentale en biologie ne pouvaient être abordées sans des connaissances approfondies en écologie, en biologie évolutive et en génétique quantitative. Il répétait cet argument, entre autres, aux réunions hebdomadaires du groupe de discussion en écologie et en évolution au département de biologie de l'université Memorial de Terre-Neuve. Les joutes oratoires qui s'engageaient entre Ram et des collègues comme Doug Morris et Jake Rice, ni l'un ni l'autre n'étant connu pour sa timidité, étaient épiques, tant par l'enthousiasme effréné qu'elles suscitaient que par l'influence incomparable qu'elles exerçaient sur plusieurs d'entre nous durant ces années de notre formation post-doctorale. C'est Ram qui, tout cela avant 1987, m'a initié à l'évolution des cycles biologiques, à la variance génétique additive, à l'épistase, à John Maynard Smith, à l'ESS, à la vraisemblance maximale, à l'APL (un langage de programmation informatique dont le seul nom d'usager au MPO était « droff », soit Derek Roff), à John Thorpe, aux caractères à seuil, à la génétique quantitative des risques, à Sewall Wright et à Ronald Fisher.

Un de mes meilleurs souvenirs des énoncés « à la Ram » est sa réaction à mon scepticisme vis à vis l'utilité et les fondements de la distinction entre les sélections *r* et *K* (un scepticisme que j'endosse encore complètement aujourd'hui) : il écrivit simplement avec sa calligraphie particulière et colorée « r-K-ic ». Parmi les milliers d'interactions que nous avons eues au cours des années qui suivirent, aucune n'incarne aussi bien que ces quatre lettres la concision, l'humour, la clarté et l'espièglerie dont Ram était toujours capable.

Contributions à la recherche et collaborations

L'étendue des intérêts de Ram pour les arts (il lisait avec avidité toutes sortes d'ouvrages, aimait le théâtre et adorait l'opéra) n'avait d'égal que la diversité des études scientifiques qu'il a entreprises. Au moment où j'écris ces lignes (décembre 2007), Ram était l'auteur ou le co-auteur de 153 publications de recherche (incluant les chapitres de livres évalués par les pairs et les articles dans la littérature scientifique primaire, mais excluant les lettres, les rapports de consultant, ainsi que les travaux de recherche et les documents de travail gouvernementaux). Il publiait principalement dans le *Journal canadien des sciences halieutiques et aquatiques*, la revue qui a fait paraître presque la moitié (46 %) de ses 98 articles scientifiques jusqu'en 2002 (47 de l'ensemble de 141 publications) (fig. 2). C'est là qu'il a publié son premier article scientifique qui explorait les méthodes d'estimer, à partir de données démographiques de poissons, la mortalité naturelle et les compromis associés (Myers and Doyle 1983), ainsi que son premier article, à titre d'auteur unique, sur le coût en survie de la reproduction chez les tacons matures mâles du saumon atlantique (Myers 1984). Il a aussi été un des auteurs de neuf contributions dans *Science* et de trois dans *Nature* (dont une réplique).

Ram collaborait bien avec d'autres chercheurs, alliant avec succès ses propres compétences en modélisation et en mathématiques aux diverses forces de ses partenaires, qui incluaient des chercheurs en sciences halieutiques, des statisticiens, des constructeurs de modèles d'évaluation des stocks, des biologistes de la conservation, des océanographes, des biologistes de terrain, des écologistes évolutifs, des naturalistes et des juristes. Par le nombre de travaux, ses

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Fig. 2. Nombre de contributions de recherche (y compris les chapitres de livres examinés par des pairs anonymes et les articles dans la littérature scientifique primaire, à l'exclusion des lettres, des rapports de consultation et des documents de recherche et de travail gouvernementaux) produites ou coproduites par Ram Myers, de 1982 à 2007. La ligne pleine représente le nombre total de contributions et la ligne brisée celles qui ont été publiées dans le *Journal canadien des sciences halieutiques et aquatiques*. Les traits horizontaux identifiés marquent l'étendue des années de publication pour les six thèmes de recherche.

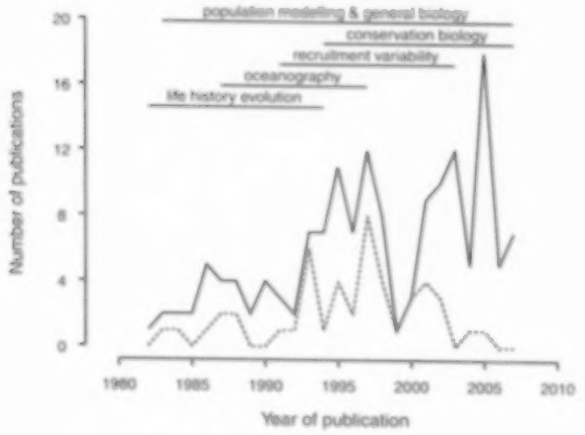
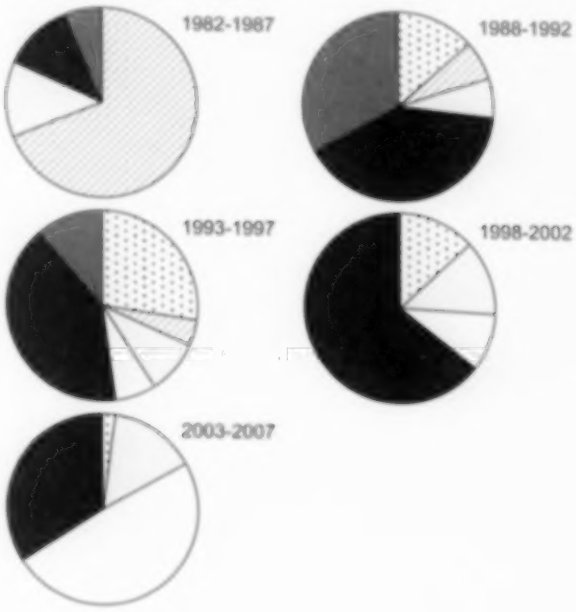


Fig. 3. Proportion des contributions de recherche de Ram Myers dans chacun des six thèmes de recherche, soit l'évolution des cycles biologiques (hachuré), l'océanographie (gris foncé), la variabilité du recrutement (pointillé), la biologie de la conservation (ouvert), la modélisation des populations (solide) et la biologie générale (gris clair).



plus importants collaborateurs furent Nick Barrowman (n = 18 publications), Jeff Hutchings (n = 16), Gordon Metz (n = 16), Mike James (n = 10) et Boris Worm (n = 9). Parmi d'autres qui ont participé à cinq ou plus publications avec lui, il faut citer Noel Cardigan, Ken Drinkwater, Jamie Gibson, Mike Hammill, Ian Jonsen, Dan Kehler, Andy Rosenberg et Gary Stenson. D'autres collaborateurs, dont Bill Montevecchi, Pierre Pépin, Jeff Runge et Peter Ward, ont chacun contribué à trois publications conjointes. Même si elle n'apparaît pas toujours de façon explicite, la contribution de ces individus, et de plusieurs autres, est intimement entrelacée dans l'ensemble de la recherche de Ram.

Carrière de chercheur

Terre-Neuve

En arrivant au MPO, Ram apprit l'existence d'un ensemble de données sur les tacons de saumons récoltées entre 1956 et 1963 dans la rivière Little Codroy (Terre-Neuve). Percevant tout de suite l'intérêt particulier de ces données, Ram entreprit d'estimer la mortalité accrue subie par les tacons mâles matures, par rapport aux mâles immatures, et la perte de productivité de saumons anadromes qui en résultait (Myers 1984). Ces analyses comprenaient une partie de son travail sur l'évolution des cycles biologiques, l'un des six thèmes dans lesquels j'ai essayé de répartir ses contributions à la recherche (fig. 3). Déjà évident dans la recherche de sa thèse de doctorat (Myers 1983), l'intérêt particulier de Ram pour l'influence des compromis reliés à la fitness sur l'évolution des cycles biologiques mena à une série d'articles publiés au milieu des années 1980 sur les tactiques reproductives de rechange chez les saumons atlantiques mâles (fig. 4). Parmi ses neufs publications faites avec d'autres et citées à plus de 100 reprises (ci-dessous les publications fréquemment citées), la première provient de cette recherche sur les cycles biologiques; c'était une des premières tentatives d'utilisation des marqueurs génétiques pour estimer le succès de la fécondation chez les poissons (Hutchings et Myers 1988).

En 1989, Ram se joignit à un petit groupe de modélisateurs et de statisticiens du MPO qui comprenait le Resource Assessment and Survey Methodology Centre of Disciplinary Expertise (RASM CODE) sous la direction de John Hoenig. Cette section devait servir de ressource nationale pour l'ensemble des chercheurs du MPO. Une des conséquences du changement de responsabilités de Ram fut une augmentation importante de la proportion de ses travaux (1988–1992) consacrés aux divers éléments de la modélisation des populations (particulièrement sur la démographie des mammifères marins), un thème de recherche qui allait prédominer pendant tout le reste de sa carrière. C'est aussi durant cette période que l'intérêt de Ram pour l'océanographie était à son plus fort. Ses travaux sur les variables environnementales explicatives de la mortalité des larves et des jeunes, par exemple, ont produit ses deux premières publications sur la variabilité du recrutement (Myers 1991; Pepin et Myers 1991), un sujet qu'il allait explorer plus à fond durant les années 1990.

La période de 1993–1997 est celle où la recherche de Ram est la plus diversifiée (fig. 3). C'est aussi la période pendant laquelle son intérêt pour le recrutement est à son

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Fig. 4. Ram debout devant le canal expérimental du ministère des Pêches et des Océans à Noel Paul's Brook, tributaire de la rivière Exploits, dans lequel lui et moi avions entrepris des travaux expérimentaux sur le saumon atlantique (octobre 1984).

maximum, alors qu'il examine comment la densité, le cycle biologique et l'océanographie affectent l'importance et l'échelle spatiale de la variabilité du recrutement. C'est à ce moment qu'ont été publiés quatre de ses articles fréquemment cités : un premier examinait l'influence de la densité sur la mortalité des jeunes chez les poissons marins (Myers et Cadigan 1993); un second présentait la première méta-analyse destinée à tester les effets d'Allee sur les relations stock–recrutement chez les poissons (Myers et al. 1995); les deux autres traitaient de l'effondrement des populations de poissons marins, en particulier de la morue franche, *Gadus morhua* (Hutchings et Myers 1994; Myers et al. 1997*a*).

Il est raisonnable de croire que l'application et l'ardeur que Ram mit dans ces derniers travaux de biologie de la conservation prirent naissance entre 1993 et 1997 lorsque nous (Ram, Nick Barrowman et moi-même) avons commencé à étudier l'effondrement des populations nordiques de morues. La perte de cette pêche commerciale, jadis extrêmement florissante, a eu et continue d'avoir des impacts énormes économiques, sociologiques et émotifs sur les terre-neuviens. Il était impossible de travailler au MPO à Terre-Neuve au début des années 1990 (comme nous le faisions tous trois) sans être conscients des obligations que les chercheurs ont vis-à-vis de la société, en particulier celle de transmettre les résultats de leur recherche à grande échelle, publiquement et honnêtement.

Tous ne partageaient pas cette vision. L'obligation morale et civique des chercheurs de communiquer les fruits de leur recherche était compromise par le désir de certains bureaucrates de contrôler l'information qui émanait du MPO vers le public. Les empêchements bureaucratiques à la communication de la science halieutique ont été discutés par Hutchings et al. (1997) qui rapportaient qu'un chercheur du MPO avait reçu une réprimande officielle pour avoir communiqué aux médias des conclusions qui correspondaient à la littérature scientifique soumise à l'examen des pairs, mais qui allaient à l'encontre des opinions véhiculées par les porte-parole du Ministère. Ce chercheur était Ram (selon un mémorandum note infrapaginale 1, Hutchings et al. 1997).

Université Dalhousie

C'est cette réprimande qui mit fin à la carrière de Ram au MPO. Selon lui, il pouvait soit se conformer et se taire, ou encore partir. Il choisit de partir et bénéficia ainsi de la liberté de parole que permettent les universités à son retour à Halifax en 1997 pour occuper la nouvelle chaire Killam en études de l'océan. Une fois à Dalhousie, Ram et le chercheur au post-doctorat Jill Casey ont réalisé leur étude de l'extraordinaire déclin des grandes raies, *Dipturus laevis*, un des plus grands poissons marins canadiens (taille maximale de 153 cm) qui s'est produit, comme Ram le disait souvent, « pendant que personne ne prêtait attention ». En effet, personne ne prenait garde parce que traditionnellement la recherche se concentrait sur les tendances temporelles des espèces ciblées directement par l'industrie de la pêche. En conséquence, les changements d'abondance des espèces capturées de façon accessoire passaient souvent inaperçus. L'intérêt accru pour les espèces de la pêche accessoire par les agences responsables de la pêche au début des années 2000 peut être attribuée en grande partie à l'intérêt suscité par l'article fréquemment cité de Casey et Myers (1998) paru dans *Science*.

Dans le sillage intellectuel des chercheurs en pêcheries Bill Ricker et Ray Beverton, ainsi que du pionnier de la modélisation des cycles biologiques, Lamont Cole, Ram affirmait avec vigueur que le taux maximal de croissance de la population est la variable la plus importante à étudier pour comprendre pleinement les facteurs qui affectent la capacité des populations de poissons à survivre à l'exploitation, à résister au déclin lors de changements imprévus du milieu et à récupérer après un effondrement. C'était ce paramètre (r_{max}) qui servait de point d'ancrage intellectuel et empirique dans beaucoup des recherches de Ram, que ce soit sur les cycles biologiques du zooplancton, sur les comportements reproductifs de rechange du saumon atlantique, sur la relation entre les abondances des parents et des rejetons dans les populations exploitées, ou sur les facteurs qui affectent l'effondrement, la récupération et le risque d'extinction chez les poissons marins.

Deux exemples de travaux influents de Ram sur la croissance maximale des populations ont été publiés en 1997 et 1999. Myers et al. (1997*b*) ont proposé des méthodes pour estimer r_{max} à partir de données de stocks–recrues; ils les ont

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Fig. 5. George Lilly (gauche), Ram (centre) et moi dans mon bureau au ministère des Pêches et des Océans à White Hills, St. John's (Terre-Neuve), lors de l'attribution du prix Wilfred Templeman (décembre 1993).

appliquées à plusieurs stocks de morues franches et ont établi de façon explicite le lien qui existe entre r_{max} et la récupération. À partir d'une analyse de plus de 700 relations reproducteurs–recrues, Myers et al. (1999; un des neuf articles fréquemment cités) ont conclu que le taux reproductif annuel maximal est relativement constant sur une gamme étendue d'espèces de poissons. Ram a qualifié ce résultat de très importante découverte (Myers et al. 1999). Un brin d'arrogance sans doute, mais dans ces circonstances, comme dans bien d'autres, il avait raison.

Dans la foulée de la banque de données de stock–recrutement que Nick Barrowman, Jessica Bridson et lui avaient compilée au milieu des années 1990 et fort d'une compréhension extraordinairement précise des techniques analytiques de modélisation, Ram a continué à traiter d'immenses ensembles de données provenant de partout sur le globe. Durant la période de cinq ans débutant en 2003, la recherche de Ram sur la biologie de la conservation a atteint un sommet. Au moment de la publication dans *Science* d'un article fréquemment cité sur le déclin des requins pélagiques dans le nord-ouest de l'Atlantique (Baum et al. 2003), tiré du travail de maîtrise de Julia Baum, Ram et Boris Worm, un chercheur au post-doctorat, ont entrepris d'estimer l'importance du déclin après les années 1950 des grandes espèces de poissons prédateurs marins ciblées par la pêche industrielle, telles que les thons et les voiliers. La conclusion des auteurs que l'océan global avait perdu plus de 90 % de ses grands poissons prédateurs, a provoqué un intérêt sans précédent pour une publication sur la biologie de la conservation marine. L'article de Myers et Worm (2003), publié dans *Nature*, est la publication de Ram qui a été le plus fréquemment citée à ce jour, ayant été mentionnée à 330 reprises; il le restera sans doute.

Il faut noter avec prudence que les travaux récents de Ram ont aussi suscité des critiques (p. ex. Walters 2003; Hampton et al. 2005; Polacheck 2006). Dans ce contexte, Ram a été mentionné comme l'un des responsable du « fossé » qui s'est creusé entre certains chercheurs en sciences halieutiques qui pensent que les déclins des populations de poissons marins ont été incorrectement exagérés et d'autres qui croient qu'il est important d'intégrer des études de la biodiversité marine aux études en sciences halieutiques (Pauly 2007). Ram aurait été d'accord avec cette caractérisation, se consolant dans l'affirmation de Winston Churchill, « Vous avez des ennemis? Bon. Cela veut dire que vous vous êtes tenu debout pour défendre un point vue, à un moment ou un autre de votre vie » [tradition]. Pendant la dernière décennie, il est devenu évident qu'il était utile d'intégrer des études de domaines typiquement associés à la biologie de la conservation (p. ex. l'écologie, la biodiversité, l'évolution, la génétique) aux travaux plus classiquement reliés aux sciences halieutiques (p. ex. les changements temporels de la mortalité due à la pêche, la variabilité du recrutement, la structure des stocks). Pauly (2007) a inventé le terme de « biologie de la conservation halieutique » pour désigner ce domaine et a nommé Ram comme l'un de ses fondateurs.

L'article de Myers et Worm (2003) a réussi à susciter un intérêt extraordinaire pour l'état critique des océans de la planète et pour le déclin de la biodiversité des poissons marins. Entre autres résultats, il permit à Ram d'avoir l'occasion de communiquer directement avec les décideurs et les politiciens; Ram servit de témoin aux audiences du

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Comité permanent des pêches et des océans de la Chambre des communes (2003, 2005) et à deux audiences de comités du Sénat des États-Unis sur la surpêche (2003). En octobre 2005, la revue *Fortune* désigna Ram comme l'une des dix personnes à garder à l'oeil (c'est-à-dire, selon la revue, des individus dont les travaux auront une influence durable) et a cité son travail sur le déclin des grands poissons prédateurs. Il y eut d'autres formes de reconnaissance du travail de Ram au cours des années; parmi les honneurs qu'on lui a décernés, citons : en 1993, le prix Wilfred Templeman (partagé avec George Lilly et moi-même; fig. 5); en 1996, une bourse de fellow invité d'Imperial College à Silwood Park (Royaume-Uni); en 1997, la première chaire Killam sur les sciences de la mer à l'Université Dalhousie; en 1999, la nomination de conférencier Great Auk à l'université Memorial de Terre-Neuve; en 2004, le prix de la société Blue Ocean pour la science de la conservation marine. Il a aussi été directeur du projet sur l'avenir des populations animales marines de la Fondation Sloan, membre du groupe des spécialistes des requins à l'Union mondiale pour la nature (IUCN), directeur scientifique d'*Ecology Letters* et membre des comités de conseillers scientifiques du Sierra Club du Canada et d'*Oceana* (Washington, D.C.).

Envoi

Quand Ram est décédé, la première chose qui m'est venue à l'esprit a été tous ces petits déjeuners pris dans mon auto. Je ne me suis jamais plaint à lui des tasses, bols et cuillers laissés sous le siège avant de ma voiture, souvent pour plusieurs jours. Le fait qu'il ne voyait rien d'anormal à utiliser mon auto comme resto avait, de manière un peu bizarre, quelque chose de touchant. Son comportement était somme toute singulier, mais je le trouvais tout de même attachant.

Quand Ram ne se sentait pas menacé, son attitude projetait la sincérité, l'honnêteté et l'innocence d'un enfant. Mais, c'est précisément l'innocence des enfants qui les rend vuinérables. C'était cette vulnérabilité sous-jacente, souvent combinée à une droiture sans compromis, et à des actes altruistes empreints de bonté, qui faisaient de Ram un être tout à fait spécial.

L'effondrement de la morue franche et d'innombrables autres poissons marins s'est produite sous notre surveillance collective sur une période étonnement courte. Les responsabilités que nous portons envers ceux qui nous suivent ne peuvent être négociables. C'était l'acceptation de ces responsabilités sociales qui expliquait la passion et l'enthousiasme que Ram mettait à son travail et la détermination avec laquelle il communiquait les résultats de sa recherche à la société.

Il y en a plusieurs qui n'étaient pas d'accord avec Ram, mais peu nieront l'impact qu'il a eu sur les sciences halieutiques et la biologie de la conservation marine. Il a mérité le respect des législateurs du Canada et des États-Unis. On salue aussi son mentorat des étudiants et sa capacité à faire connaître à grande échelle et de façon claire l'état critique des océans. Notre société a bénéficié de ses provocations et de ses rappels à l'ordre, toujours fondés sur ses connaissances scientifiques. Tout cela nous a forcés à examiner nos océans avec plus d'attention, à tirer profit de nos erreurs du passé et à reconnaître que le maintien de la santé et de la biodiversité des écosystèmes marins était une priorité et une responsabilité fondamentale vis-à-vis des générations futures. Nous n'avons ni les moyens ni le droit d'ignorer ces problèmes.

Ram Myers était mon collègue, mon confident et mon ami et il me manque terriblement. Il laisse dans le deuil sa conjointe Rita Kindl Myers et leurs enfants Emily, Rosemary, Sophia, Carlo et Gioia, ainsi que son frère Abbot Myers et ses soeurs Joan Peters et Susan Myers.

Bibliographie

Baum, J.K., Myers, R.A., Kehler, D.G., Worm, B., Harley, S.J. et Doherty, P.A. 2003. Collapse and conservation of shark populations in the Northwest Atlantic. Science (Washington, D.C.), **299**: 389–392.

Casey, J.M. et Myers, R.A. 1998. Near extinction of a large, widely distributed fish. Science (Washington, D.C.), **281**: 690–692.

Hampton, J., Sibert, J.R., Kleiber, P., Maunder, M.N. et Harley, S.J. 2005. Fisheries: decline of Pacific tuna populations exaggerated? Nature (London), **434**: E1–E2.

Hutchings, J.A. et Myers, R.A. 1988. Mating success of alternative maturation phenotypes in male Atlantic salmon, *Salmo salar*. Oecologia, **75**: 169–174.

Hutchings, J.A. et Myers, R.A. 1994. What can be learned from the collapse of a renewable resource? Atlantic cod, *Gadus morhua*, of Newfoundland and Labrador. Can. J. Fish. Aquat. Sci. **51**: 2126–2146.

Hutchings, J.A., Walters, C. et Haedrich, R.L. 1997. Is scientific inquiry incompatible with government information control? Can. J. Fish. Aquat. Sci. **54**: 1198–1210.

Myers, R.A. 1981. The evolution of dispersal in a stochastic environment. Mémoire de maîtrise, Université Dalhousie, Halifax (Nouvelle-Écosse).

Myers, R.A. 1983. The use of inverse optimization in evolutionary biology. Thèse de doctorat, Université Dalhousie, Halifax (Nouvelle-Écosse).

Myers, R.A. 1984. Demographic consequences of precocious maturation of Atlantic salmon (*Salmo salar*). Can. J. Fish. Aquat. Sci. **41**: 1349–1353.

Myers, R.A. 1991. Recruitment variability and range of three fish species. NAFO Sci. Counc. Stud. **16**: 21–24.

Myers, R.A. et Cadigan, N.G. 1993. Density-dependent juvenile mortality in marine demersal fish. Can. J. Fish. Aquat. Sci. **50**: 1576–1590.

Myers, R.A. et Doyle, R.W. 1983. Predicting natural mortality rates and reproduction — mortality trade-offs from fish life history data. Can. J. Fish. Aquat. Sci. **40**: 612–620.

Myers, R.A. et Worm, B. 2003. Rapid worldwide depletion of predatory fish communities. Nature (London), **423**: 280–283.

Myers, R.A., Barrowman, N.J., Hutchings, J.A. et Rosenberg, A.A. 1995. Population dynamics of exploited fish stocks at low population levels. Science (Washington, D.C.), **269**: 1106–1108.

Myers, R.A., Hutchings, J.A. et Barrowman, N.J. 1997*a*. Why do fish stocks collapse? The example of cod in eastern Canada. Ecol. Appl. **7**: 91–106.

Myers, R.A., Mertz, G. et Fowlow, S.P. 1997*b*. Maximum population growth rates and recovery times for Atlantic cod (*Gadus morhua*). Fish. Bull. **95**: 762–772.

Myers, R.A., Bowen, K.G. et Barrowman, N.J. 1999. Maximum reproductive rate of fish at low population sizes. Can. J. Fish. Aquat. Sci. **56**: 2404–2419.

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Pauly, D. 2007. Obituary: Ransom Aldrich Myers (1952–2007). Nature (London), **447**: 160.

Pepin, P. et Myers, R.A. 1991. Significance of egg and larval size to recruitment variability of temperate marine fish. Can. J. Fish. Aquat. Sci. **48**: 1820–1828.

Polacheck, T. 2006. Tuna longline catch rates in the Indian Ocean: did industrial fishing result in a 90% rapid decline in the abundance of large predatory species? Marine Policy, **30**: 470–482.

Walters, C.J. 2003. Folly and fantasy in the analysis of spatial catch rate data. Can. J. Fish. Aquat. Sci. **60**: 1433–1436.

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Ecological change in Great Lakes communities — a matter of perspective[1]

W. Gary Sprules

Abstract: Enormous change in food webs of the Laurentian Great Lakes has been documented from the early 1970s to the 1990s. Variation in abundances of species at all levels in these food webs has been attributed to a variety of causes, including nutrient abatement, invasive species, fishing practices, and climate change. However, this impression of great change is not obvious if food webs are examined from the different perspective of the biomass size spectrum. Despite large shifts in the species structure of zooplankton communities in Lakes Erie and Ontario from 1991 to 1997, zooplankton size spectra have not changed. Furthermore, size spectra for complete food webs of Lake Ontario (Laurentian Great Lake) and Lake Malawi (African Rift Valley Lake) are statistically indistinguishable despite enormous contrast in the geological age and fauna of the two lakes. I conclude that constraints on bioenergetic rate processes and physiological and ecological similarities of like-sized organisms at various hierarchical levels of organization lead to regular and repeatedly observed emergent properties of aquatic ecosystems that are independent of specific species.

Résumé : Des changements considérables ont été observés dans les réseaux alimentaires des Grands Lacs laurentiens depuis le début des années 1970 jusqu'aux années 1990. On a tenté d'expliquer la variation dans l'abondance des espèces par un ensemble de causes dont la réduction des nutriments, les espèces envahissantes, les pratiques de pêche et le changement climatique. Cependant, cette impression de changement majeur est moins évidente lorsqu'on examine les réseaux alimentaires du point de vue des spectres de biomasse en fonction de la taille. Malgré d'importants changements dans la structure spécifique des communautés de zooplancton des lacs Érié et Ontario de 1991 à 1997, les spectres de taille du zooplancton n'ont pas varié. De plus, le spectre de taille de l'ensemble du réseau alimentaire du lac Ontario, un Grand Lac laurentien, et celui du lac Malawi, dans le rift africain, ne peuvent être distingués statistiquement, malgré les différences énormes d'âge géologique et de faune entre les deux lacs. En conclusion, les contraintes sur les taux des processus bioénergétiques et les ressemblances physiologiques et écologiques d'animaux de tailles semblables aux divers niveaux hiérarchiques de l'organisation expliquent l'existence de propriétés émergentes régulières et souvent observées dans les écosystèmes aquatiques qui sont indépendantes de la présence d'espèces particulières.

[Traduit par la Rédaction]

Introduction

Ecosystems of the Laurentian Great Lakes have changed greatly since the early 1970s when a workshop entitled Salmonid Communities in Oligotrophic Lakes (SCOL) was convened to evaluate the integrity of these important ecosystems (Loftus and Regier 1972). An analysis of these changes from the early 1970s to the late 1990s at a follow-up series of workshops (SCOL2, Hansen and Kerr 2004) attributed change to a number of factors, including cultural eutrophication, fish harvesting, invasive species, global warming, and contaminants (Madenjian et al. 2002; Bronte et al. 2003; Dobiesz et al. 2005). Some alterations, such as reduced phosphorus loadings and associated improvements in water quality (Mills et al. 2003) and recent reductions in contaminant loadings (DeVault et al. 1996), have been positive. Other alterations, such as increasing numbers of invasive species (Ricciardi and Atkinson 2004) and fish harvesting (Koonce et al. 1999), are of increasing concern and expense (Colautti et al. 2006).

Biological changes in the Great Lakes during the periods covered by the SCOL studies have been documented principally through analyses of patterns in abundances of species through time. Native lake trout (*Salvelinus namaycush*) declined in most of the lakes because of over-harvesting and the invasion of sea lamprey (*Petromyzon marinus*) but were

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[1]This paper forms part of the proceedings of a workshop convened at the University of Toronto Mississauga, 18–20 May 2000. The workshop was sponsored by the Great Lakes Fishery Commission to revisit Great Lakes ecosystem change, three decades since the first Salmonid Communities in Oligotrophic Lakes (SCOL) Symposium, which was convened at Geneva Park, Ontario, in July 1971 and for which the proceedings were subsequently published as a special issue of the Journal of the Fisheries Research Board of Canada (Volume 29, Number 6, June 1972). The first paper in the SCOL2 series (Madenjian et al. 2002) was previously published in this journal.

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replaced through stocking of Pacific salmon that have become very abundant (Madenjian et al. 2002). The alewife (*Alosa pseudoharengus*), an exotic planktivore, cycled in abundance enormously because of its sensitivity to unusually cold conditions during spring, with associated impacts on many invertebrate and other fish species (Rand et al. 1995; Rand and Stewart 1998). The species composition of zooplankton and benthic invertebrate communities varied in response to changes in fish predators and the introduction of exotic invertebrates such as dreissenid mussels (*Dreissena* spp.) and the carnivorous *Bythotrephes longimanus* and *Cercopagis pengoi* (Johannsson et al. 1991; Lehman and Caceres 1993; Benoit et al. 2002). Reasons for variation in the taxonomic composition of algal communities is more difficult to assess but is partly due to shifting nutrient conditions (Millard et al. 2003; Conroy et al. 2005) and changes in zooplankton grazers (Johannsson 2003; Barbiero et al. 2006).

Temporal variation in abundances of individual species is only one of many criteria for evaluating ecosystem change, but is understandably important because of the dependency of commercial and sports fisheries on particular species. Have Great Lakes communities really changed as much as species data indicate? Would other scales of observation or indices of ecosystem structure reveal a different perspective? For instance, despite the collapse of lake trout fisheries in Lakes Michigan and Ontario, a profitable and extensive harvest of Pacific salmonids now exists in both lakes (Bence and Smith 1999; Stewart et al. 2003.). Biological communities are organized at hierarchical levels (O'Neill et al. 1986), and patterns of whole communities cannot be predicted solely from information on individual species (Rosen 1991). Community characteristics at more integrative levels of observation could include primary productivity, ratios of predatory to herbivorous species (Cohen 1977), particle size spectra (Kerr and Dickie 2001), or measures of throughput or ascendancy from network theory (Ulanowicz 2003). Such community characteristics emerge despite large numbers of unique individual species interacting in complex, unpredictable ways at varying temporal and spatial scales and may persist despite external perturbation.

To test these assertions about emergent community properties, I use one particular integrative measure, the biomass size spectrum, to quantify variation in the structure of zooplankton communities of Lakes Ontario and Erie during a period of extensive perturbation and contrast this with published information on species changes during the same period. I use the same approach to compare the structure of the pelagic community of a young, temperate North American lake (Lake Ontario) with an ancient, tropical African lake (Lake Malawi). These analyses indicate little or no differences in size structure despite extensive perturbation and differences in species composition, thereby supporting the concept of emergent community properties that are resilient to perturbation and the dynamics of component species.

Materials and methods

Field methods

Data were collected during a series of sampling cruises on Lakes Erie and Ontario from 1991 to 1997 on the CSS *Limnos* (Figs. 1*a* and 1*b*, Table 1). Although spatial and temporal coverage varied among lakes and years, I tried to produce consistent data sets appropriate for comparison. All zooplankton data were collected with an optical plankton counter (OPC1-T, Focal Technologies, Dartmouth, Nova Scotia, Canada) mounted on a V-Fin towbody (Endeco-YSI, Marion, Massachusetts, USA), an Aquatracka fluorometer (Chelsea Technologies Group, West Molesey, Surrey, UK), a conductivity–temperature–depth probe (OS-200, Ocean Sensors Inc., San Diego, California, USA), and a digital flow meter (model 2031, General Oceanics, Miami, Florida, USA).

The OPC comprises a 51.2 cm sampling tunnel with a 2 cm × 22 cm opening (reduced to 2 cm 6.2 cm with an acrylic insert to minimize coincident counts) across which a collimated light beam 4 mm × 20 mm in cross-section passes (Herman 1992). Zooplankton from ~0.25 to 25 mm are detected as they pass through the light beam while the OPC is being towed, and their size and frequency are recorded. Size is determined from a voltage change caused by the occlusion of light as an animal passes through the light beam and is recorded as equivalent circular diameter (ECD, the diameter of a circle blocking the same amount of light). Body sizes and numbers of individual zooplankton encountered were recorded every second, which corresponds to a linear distance of ~2.5 m and a volume of 3.1 L at a tow speed of 2.5 $m \cdot s^{-1}$. Body size and concentration were adjusted to account for coincident counts typical of high organism concentrations like those in Lakes Ontario and Erie (Sprules et al. 1998; Morris 2002).

Instruments were towed in a continuous undulating pattern from near surface to depth as the ship moved along linear sampling transects that ranged from 1.7 to 22.8 km (median = 9.2 km). Each transect constituted a single observation. Depths shallower than 2 m were excluded to avoid artefacts caused by surface bubbles and disturbance. Maximum sampling depth was restricted to roughly 100 m by the hydrodynamic characteristics of the towbody, and the instruments were never towed closer than 5 m to the substrate. All data were collected at night (from approximately 1100 to 0500) to ensure adequate sampling of migratory species such as *Mysis relicta*.

Data processing

All zooplankton encountered during a single transect were combined, and the total volume of water sampled was calculated. The biovolume of each animal was calculated as the volume of a prolate spheroid with major axis equal to the ECD and an aspect ratio of 1.33:1 (major:minor axis) for Lake Ontario (Sprules et al. 1998) and 1.96:1 for Lake Erie (Morris 2002). The different aspect ratios reflected the differing taxonomic compositions of the lakes and were determined through comparisons of zooplankton biomass and size distributions obtained by plankton nets with those from the OPC (Sprules et al. 1998). Biovolume was converted to body mass (fresh g) assuming a specific gravity of unity. The biomass size spectrum for each transect was calculated from these data by grouping all individuals into a $\log_2$ series of mass intervals, summing the body masses for each interval, and dividing by the volume of water sampled to give the biomass concentration (fresh $g \cdot m^{-3}$) in each mass interval.

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Fig. 1. Maps of Lakes Ontario (*a*) and Erie (*b*) showing sampling transects (lines) and the fixed stations (circles) at the ends of the transects.

Spectral density (m^{-3}) for each mass interval was then computed by dividing the biomass concentration ($g \cdot m^{-3}$) by the width of the mass interval (g), and the biomass size spectrum was presented as a logarithmic plot of spectral density against body mass (e.g., Fig. 2*a*). For a $\log_2$ series of mass intervals, the width of an interval is the same as the lower limit of the interval (e.g., 8–16 g, width = 8). Spectral density is therefore biomass concentration ($g \cdot m^{-3}$) divided by a nominal organism mass (g), which is roughly equivalent to organism concentration ($number \cdot m^{-3}$).

Biomass size spectra were also constructed for the complete pelagic communities (phytoplankton, zooplankton, fish) of Lake Ontario and Lake Malawi to illustrate size structural similarities of these very different ecosystems. Data for Lake Ontario are from Sprules and Goyke (1994). In summary, data on size and abundance of pelagic phytoplankton, zooplankton, and fish and the benthic amphipod *Diporeia hoyi* were collected on three lake-wide research cruises during May, August, and November 1990. Integrated water column samples of phytoplankton and vertical plankton net hauls of zooplankton were from fixed stations where organisms were microscopically enumerated and sized. *Diporeia hoyi* size and density were determined from benthic Ponar samples at fixed stations. A combination of hydroacoustics and midwater and bottom trawl nets were used to obtain data on fish abundance and size. The mean annual size spectrum was determined by averaging the biomass of organisms from the three cruises in a $\log_2$ series of mass intervals, as described above.

Data for Lake Malawi, from Allison (1996), were collected similarly. Ten lake-wide sampling surveys were conducted between June 1992 and April 1993. Phytoplankton were sampled at fixed stations with a string of water bottles and examined microscopically. Zooplankton, the midge larva *Chaoborus edulis*, and the cyprinid fish *Engraulicypris sardella* were collected by oblique tows of high-speed plankton nets at fixed stations and examined microscopically (zooplankton) and either weighed in replicated batches (*C. edulis*) or sized through length–weight relationships (*E. sardella*). Other fish densities and sizes were determined through a combination of midwater trawls at fixed stations and acoustically along a zigzag grid of transects over the whole lake. The biomasses of organisms in a $\log_2$ series of mass intervals from each cruise were averaged to produce an annual size spectrum. In the original Lake Malawi and Lake Ontario studies, spectral density was expressed on an areal

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Table 1. Linear distances (km) sampled during each research cruise.

Lake	Year	Month	Region			Sum
			West	Central	East	
Ontario	1991	July	—	60.1	—	60.1
		November	42.2	60.4	—	102.6
	1992	May	—	20.9	—	20.9
	1993	September	—	9.5	—	9.5
	1995	July	18.6	64.3	74.6	157.5
		October	—	—	7.8	7.8
	1996	April	38.7	35.4	36.5	110.6
	1997	October	48.7	—	—	48.7
Sum			148.2	250.6	118.9	517.7
Erie	1992	July	11.2	28.2	7.2	46.6
	1993	June	26.3	66.1	52.9	145.3
		September	25.1	—	—	25.1
	1994	May	12.1	33.3	56.9	102.3
		September	53.4	119.4	85.5	258.3
	1995	May	—	77.8	19.5	97.3
	1996	July	36.2	118.5	—	154.7
	1997	September	—	—	13	13
Sum			164.3	443.3	235	842.6

Note: These distances comprise varying numbers of individual transects (median length = 9.2 km) that comprise the replicate observations of the study.

(m^{-2}) rather than volumetric basis, and these units have been retained.

Statistical analyses

To test whether the shapes of biomass size spectra differed among years, I used Kolmogorov–Smirnov two-sample tests (Zar 1999) with Bonferroni adjustments to the critical probability value to avoid inflation of the Type I error rate (adjusted p value = 0.05/number of tests). I used analysis of covariance to test the hypothesis that linear regressions fitted to the size spectra for the complete food webs of Lakes Ontario and Malawi did not differ (Zar 1999). These linear models are approximate only since spectral density is not independent of body size, and a linear trend is only a rough descriptor of the trend in spectral density across body size.

Results

For Lake Ontario, mean zooplankton biomass spectra differed little from 1991 to 1997 (Fig. 2*a*). Each spectrum comprised two spectral "domes" (sensu Thiebaux and Dickie 1993) that merged at a body mass of roughly $10^{-2.8}$ or 0.0016 g. The dome below this mass comprised smaller zooplankton groups such as the cyclopoid copepods and bosminid cladocerans, whereas the other dome contained larger species such as the hypolimnetic calanoid copepods *Senecella calanoides* and *Limnocalanus macrurus* and the opossum shrimp *M. relicta*. No consistent changes are obvious in the spectra throughout the study period, and all pairwise comparisons failed to reject the hypothesis that biomass spectra were similar from 1991 to 1997 (all $p \geq 0.16$, Kolmogorov–Smirnov two-sample tests). Statistical uncertainty of the mean spectral values varied with body mass interval, but the median value of the standard error was 0.09 (log m^{-3}), with most values from 0.07 to 0.13 (Fig. 2*a*). This variation was small compared with interannual variability in spectral density (roughly 1.0 log m^{-3}). Restricting the analysis to the most consistently and intensively sampled central transect (Table 1) indicated a similar pattern that showed two domes corresponding to larger and smaller organisms but with somewhat greater interannual variation (Fig. 2*b*). In particular, size spectra from spring samples (May 1992, April 1996) when peak community development may not have yet occurred showed greater spectral density of small organisms and lower spectral density of larger organisms (Fig. 2*b*), but there were no statistical differences between pairs of spectra ($p \geq 0.26$).

For Lake Erie, mean zooplankton biomass spectra showed similar patterns of minimal variation in structure from 1992 to 1997 (Figs. 3*a* and 3*b*). A single spectral dome existed for Lake Erie, and the upper size limit of organisms was smaller than in Lake Ontario (roughly 2 mg compared with 32 mg) principally due to the absence of *M. relicta*. Pairwise comparisons of Lake Erie spectra (Fig. 3*a*) indicated no significant differences in spectral density among years ($p \geq 0.66$, Kolmogorov–Smirnov two-sample test). Spectra from the more consistently and intensively sampled central basin (Fig. 3*b*) during 1994–1996 were similar in pattern, although spectral density varied more among years for organisms larger than ~0.3 mg (log mass = –3.6). Patterns of spectral density did not differ significantly among years ($p \geq 0.66$, Kolmogorov–Smirnov two-sample test).

Size spectra for the pelagic communities of Lakes Ontario and Malawi were remarkably similar (Fig. 4*a*). Both lakes showed declines in spectral density with increasing body size, and both comprised a series of spectral domes corresponding to major taxonomic groupings. Relationships between the two lakes in the location and height of body size biomass peaks were clearer in non-normalized size spectra (Fig. 4*b*). Spectral densities of the two lakes (Fig. 4*a*) were intermingled across a range of organism sizes, and overall shapes of the distribu-

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Fig. 2. Mean zooplankton biomass spectra for Lake Ontario for various years using transects from the whole lake (*a*) and from only the central transect (*b*). Standard errors (SEs) of mean spectral density for each size class are not shown to minimize clutter, but twice the median SE of 0.09 on either side of a midpoint is shown in panel (*a*) (two-thirds of the SEs fell between 0.065 and 0.125). Solid triangles, 1991; open triangles, 1992; solid circles, 1993; open circles, 1995; solid squares, 1996; and open squares, 1997.

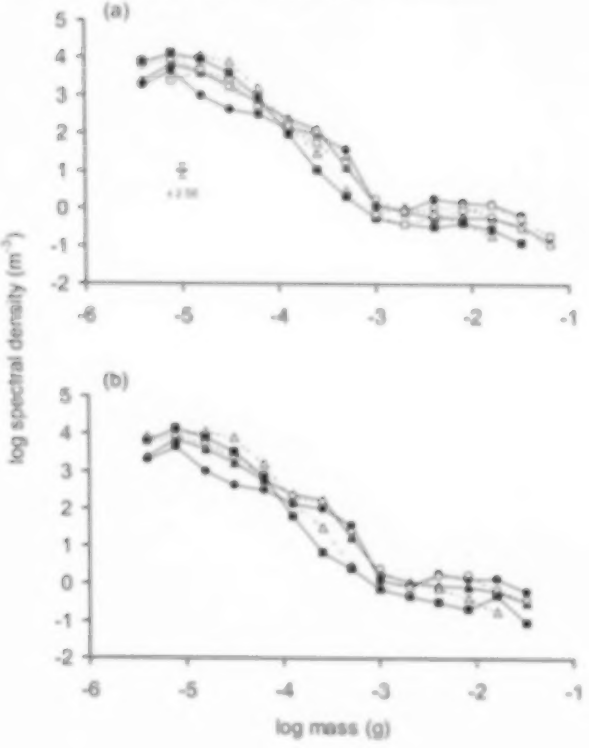
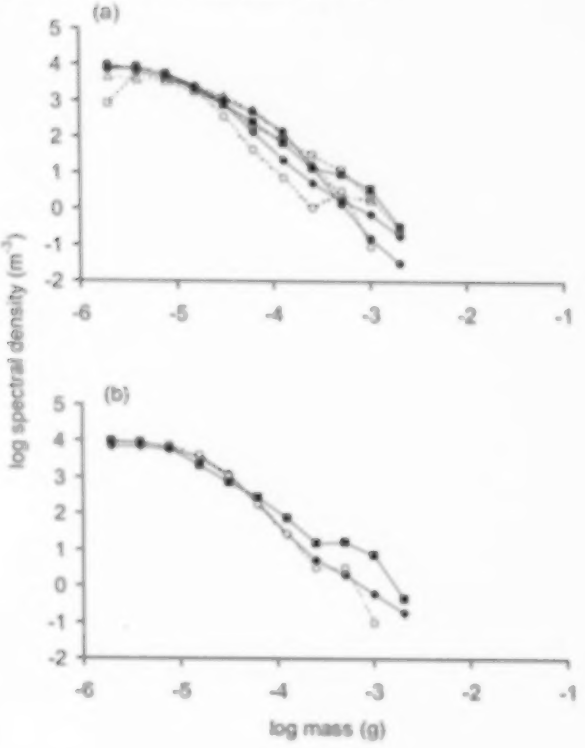


Fig. 3. Mean zooplankton biomass spectra for Lake Erie for various years using transects from the whole lake (*a*) and from only the two western-most transects from the central basin (*b*). Solid triangles, 1991; open triangles, 1992; solid circles, 1993; solid diamonds, 1994; open circles, 1995; solid squares, 1996; open squares, 1997. No standard errors are shown.



tions did not significantly differ (Kolmogorov–Smirnov two-sample test, maximum difference = 0.188, two-tailed p = 0.324). However, the spectral density in Lake Ontario was slightly higher than that in Lake Malawi (Fig. 4*a*). Linear models that described most of the variation in the spectral densities of both lakes indicated no difference in slopes but a significant difference in adjusted mean log spectral densities (Table 2). Therefore, the spectral density in Lake Ontario was $10^{3.79-3.22}$ = 3.7 times greater than that in Lake Malawi, which means that organism concentration in Lake Ontario was roughly 3.7 times greater.

Discussion

Biomass size spectra of zooplankton communities in Lakes Ontario and Erie suggested that size structure changed very little over the period 1991–1997. Limited variation in the overall form of the size spectrum for either lake indicated that the same size groups of zooplankton persisted among years and that relative abundances of the size groups changed very little through time. The spectra of the two lakes differed somewhat, due principally to the presence of the large-bodied *M. relicta* in Lake Ontario, but the community structure of both lakes was relatively stable through time.

Stability of zooplankton size spectra in Lakes Erie and Ontario contrasted markedly with ecosystem changes in the two lakes during and preceding 1991–1997. For example, reductions in phosphorous loadings from the 1970s to the 1990s mandated under the Great Lakes Water Quality Agreement and invasions of exotic mussels of the genus *Dreissena* caused oligotrophication of both lakes (Negley et al. 2003). Reductions in phytoplankton biomass and shifts in the composition and seasonal succession of the community, particularly in nearshore regions, were associated with increases in abundance of the mussels. An historically dominant benthic species, the amphipod *Diporeia*, all but disappeared from eastern Lake Erie (Dermott and Kerec 1997) and many regions in the eastern part of Lake Ontario (Dermott 2001) as dreissenid mussels populations increased rapidly and spread from shallow to deeper regions of the lakes. This lipid-rich amphipod was an important prey for fish species such as the lake whitefish (*Coregonus clupeaformis*), rainbow smelt (*Osmerus mordax mordax*), and alewife. Fish communities of both lakes have undergone fluctuations in species composition and abundance: in Lake

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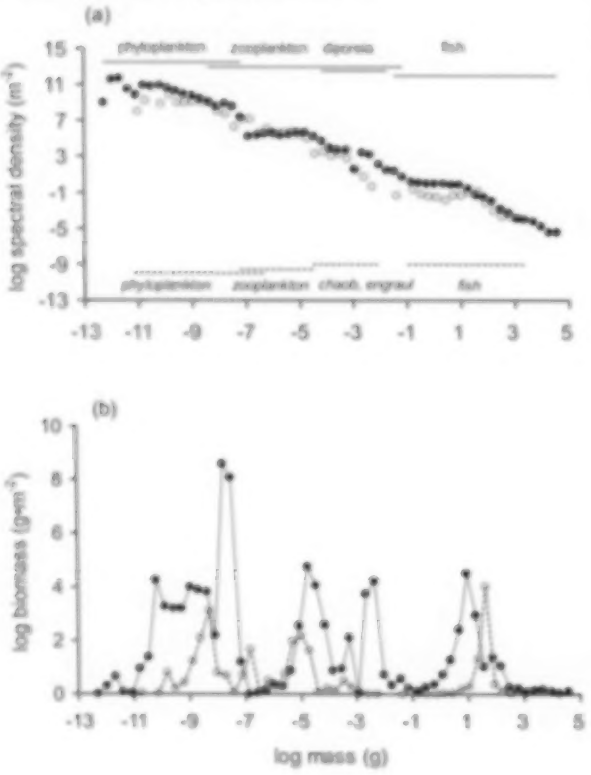

Fig. 4. Biomass size spectra for the complete food webs of Lakes Ontario (solid circles) and Malawi (open circles). Spectra are annual averages. Panel (*a*) shows the normalized spectra; panel (*b*) shows the non-normalized spectra. The dominant trophic groups–species, and the approximate size ranges they occupy are shown for Lake Ontario (solid horizontal lines and labels) and for Lake Malawi (broken horizontal lines and italicized labels). Chaob refers to the midge *Chaoborus edulis* and engraul to the cyprinid *Engraulicypris sardella*. Data for Lake Ontario reprinted with the permission of NRC Research Press, Canada (Sprules and Goyke 1994), and for Lake Malawi with the permission of Blackwell Publishing, United Kingdom (Allison 1996).

Ontario because of extensive stocking of non-native Pacific salmonids and extreme cycles in abundance of alewife (Mills et al. 2003); and in Lake Erie because of physical changes in nearshore habitat induced by *Dreissena* and variations in abundance of top predators such as walleye (*Sander vitreus*) (Ryan et al. 1999).

Substantial changes in zooplankton communities were associated with food-web variations in both lakes during the study period 1991–1997. In Lake Ontario, zooplankton productivity increased at an offshore station but declined at a nearshore station, and the total zooplankton biomass, particularly of cladocerans and cyclopoid copepods, increased (Johannsson 2003). Typically associated with more nutrient-rich waters, the small herbivorous cladoceran, *Chydorus sphaericus*, disappeared from the Kingston Basin and main lake in the early 1990s owing undoubtedly to long-term declines in phosphorous concentrations and primary productivity (Johannsson 2003). The invasive predatory invertebrate, *B. longimanus*, appeared in noticeable numbers during 1994 for only the second time since its invasion in 1982. Veliger larvae of the invasive mussels *Dreissena polymorpha* and *Dreissena bugensis* were first found in alewife guts in 1992 and 1993 and increased steeply in abundance in the Kingston Basin in 1995 to reach 39% of combined veliger and zooplankton production (Johannsson 2003). In Lake Erie, variations are more complex because of differences among basins and between nearshore and offshore regions. Annual late-summer densities of the predatory cladocerans *B. longimanus* and *Leptodora kindtii* fluctuated up to 100- and 200-fold, respectively, during the study period in the central and east basins (Barbiero and Tuchman 2004). The herbivorous cladocerans *Daphnia longiremis* and *Bosmina longirostris* also fluctuated greatly in abundance, particularly *B. longirostris*, which varied 6000-fold in the east basin (Barbiero and Tuchman 2004). Johannsson et al. (1999) documented a general increase in zooplankton biomass of about 45% and mean length of 35% from 1991 to 1995 at an offshore site in the east basin, but in 1996 both declined back to 1991 values. Despite these extensive shifts in the character and productivity of the Lakes Ontario and Erie zooplankton communities, I detected no significant changes in zooplankton biomass size spectra.

I also found that the size spectra for the whole pelagic communities of Lakes Ontario and Malawi were remarkably similar. These lakes are both large in physical size, but are otherwise completely different. Lake Ontario is a temperate North American lake that is geologically young (<10 000 years) and contains relatively few species, many of which are recent invaders from elsewhere. In contrast, Lake Malawi is a tropical African lake that is geologically old (10–20 million years old; Bootsma and Hecky 2003) and contains 500–1000 fish species, most of which are endemic, with benthic and pelagic invertebrate communities similar in diversity to the Laurentian Great Lakes (Allison 1996; Bootsma and Hecky 2003). Except for an overall lower abundance of organisms in Lake Malawi that is most likely due to sampling design, the size spectra of the two lakes were remarkably similar. The lower abundance is simply because the sampling effort in Lake Malawi was focussed on offshore pelagic regions that have very low concentrations of organisms (E.H. Allison, School of Development Studies, University of East Anglia, Norwich NR4 7TJ, UK, personal communication), whereas sampling in Lake Ontario included offshore as well as nearshore areas. Hecky (1984) presents an analysis of trophic structure and carbon transfer efficiencies for a number of large tropical lakes, including Malawi, and concludes that freshwater systems do not conform to the structural regularities I have identified here. However, it is important to recognize that his analysis was based on trophic pyramids rather than body size and hence do not directly address the patterns in spectral density evident in the observations I have presented.

Why has biomass size structure of the zooplankton communities of Lakes Erie and Ontario changed so little during 1990–1996, despite major food-web perturbations, and why are lakes as different as Ontario and Malawi so similar in their biomass size structures? Such regularities are most likely the result of physiological and ecological limits on the

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Table 2. Comparisons of linear models fitted to the Lake Malawi and Lake Ontario biomass spectra ($\log S = c + b \times \log M$, where S is spectral density and M is mass).

	Lake Malawi	Lake Ontario	ANCOVA
Linear regression			
b	–1.04 (0.03)	–1.02 (0.02)	$F_{[1,97]} = 0.09$, $p = 0.76$
c	–0.82 (0.19)	–0.20 (0.14)	
Explained variance	96%	97.5%	
Adjusted mean	3.22	3.79	$F_{[1,98]} = 11.2$, $p = 0.001$

Note: Standard errors are shown in parentheses. In the analysis of covariance (ANCOVA), the dependent variable is log S, the covariate is log M, and the fixed factor is lake. Adjusted means are means of log S adjusted for linear dependency on log M.

transfer and dissipation of energy through the size-structured food webs so typical of aquatic systems (Kerr and Dickie 2001). For a food web in any particular region, the annual flux of primary energy in the form of solar radiation is relatively fixed. Along with nutrient supplies, this sets the level of primary productivity that supplies the whole food web through a series of consumption, growth, respiration, and decomposition events at the level of individual species. The rates of most of these processes are size-dependent (Peters 1983) and fall within relatively narrow limits. For example, the coefficient of the power relationship between body mass and standard metabolic rate for 33 observations on poikilothermic organisms ranging from 10^{-6} to 100 kg in mass was 0.751 with a standard error of 0.015 (Hemmingsen 1960, cited in Peters 1983). In addition to limits on such fundamental physiological rate processes at the level of the individual organism, there are also regularities in many ecological processes at the level of populations. The exponent of the specific rate of population production (production/biomass) as a function of body mass for a wide range of organisms falls close to –0.25 (Peters 1983). In aquatic ecosystems, predator size tends to be a relatively constant multiple of prey size (Sheldon et al. 1977; Peters 1983; Pearre 1986), with predators uniformly larger than their prey. Population density and size distribution of prey strongly limits the growth efficiency of individual predators. As predators grow in body size relative to their prey or as prey concentration decreases through mortality or reduced spatial–temporal overlap with predators, increasing amounts of energy are expended to capture smaller and rarer prey, with resultant declines in growth efficiency (Pazzia et al. 2002; Kaufman et al. 2006). However, if the predator reaches a size sufficient for the capture of larger prey, growth efficiency increases sharply and begins a slow decline as predators continue to grow in relative size (Paloheimo and Dickie 1965; Sherwood et al. 2002).

Variability in these physiological and ecological processes is greatest among individual organisms, and properties of a whole system are difficult to predict solely from knowledge of individuals. However, the degree of such variability depends on the level of organization. Organisms of like size, for instance, have more similar metabolic rates, as noted above. Furthermore, similar-sized organisms in lakes tend to feed at similar trophic levels, so their energy supply and predation risk are more similar than developmental stages within a species that feed at varying trophic levels. Such limits on bioenergetic rate processes and the physiological and ecological similarities of like-sized organisms at various hierarchical levels of organization in aquatic ecosystems (Kerr and Dickie 2001) lead to emergent properties of aquatic food webs that are independent of the particular species present. Such properties are evident in the biomass size spectra for lakes presented here, despite obvious and undoubtedly important changes in zooplankton species compositions of Lakes Erie and Ontario and large differences in the fauna of Lakes Ontario and Malawi. Of course, these organisational constraints do not mean that ecosystems are immutable, since gaps and truncations in size distributions that affect production efficiency can arise because of external perturbations such as intense harvesting.

Gamble et al. (2006) explored the sensitivity of a variety of statistical models based on the zooplankton biomass size spectrum to environmental changes in Oneida Lake, New York State. Their results were mixed, with only some zooplankton size descriptors being related to some environmental variables. Based on the arguments I have developed here, minimal changes in zooplankton size spectra are expected as lake environments vary because of regularities in size structure resulting from ecological and physiological constraints. Gamble et al. (2006) point out that the general similarity in size spectra noted for a wide range of ecosystems indicates a "basic underlying ecosystem condition or pattern". In a similar study, Yurista et al. (2005) were successful in discriminating zooplankton assemblages among Lakes Superior, Michigan, Huron, and Erie based on statistical descriptors of zooplankton biomass domes. It is not unexpected that differences in size structure may be observed when lake features such as productivity or morphometry differ substantially, but it must be cautioned that the Yurista et al. (2005) analyses were based on very limited spatial and temporal sampling, so that the mean state of these systems may not have been adequately quantified.

In summary, analyses of Laurentian Great Lakes communities from the 1970s to the 1990s undertaken during the SCOL2 series of workshops (Madenjian et al. 2002; Bronte et al. 2003; Dobiesz et al. 2005) identified a large number of major shifts in species composition and community interactions and attributed these shifts to a combination of natural and human disturbances. Many of these species shifts, such as variation in the abundances of commercially valuable fish species in Lake Erie, have important economic consequences and in this sense are profound. Nevertheless, higher-order, body-size-dependent bioenergetic and ecological processes manifest as spectral regularities in biomass of these ecosystems, or at least the zooplankton subcomponent of them, have not changed. Further, Lakes Ontario and Malawi,

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which differ greatly in physical, chemical, and biological properties, are remarkably similar in their biomass size spectra. Even though species differ, the functionality of these large ecosystems remains intact.

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References

Allison, E.H. 1996. Estimating fish production and biomass in the pelagic zone of Lake Malawi/Niassa: a comparison between acoustic observations and prediction based on biomass size-distribution theory. *In* Stock assessment in freshwater fisheries. *Edited by* I.G. Cowx. Fishery News Books, Blackwell Science, Oxford, UK. pp. 224–242.

Barbiero, R.P., and Tuchman, M.L. 2004. Changes in the crustacean communities of Lakes Michigan, Huron, and Erie following the invasion of the predatory cladoceran *Bythotrephes longimanus*. Can. J. Fish. Aquat. Sci. **61**: 2111–2125.

Barbiero, R.P., Rockwell, D.C., Warren, G.J., and Tuchman, M.L. 2006. Changes in spring phytoplankton communities and nutrient dynamics in the eastern basin of Lake Erie since the invasion of *Dreissena* spp. Can. J. Fish. Aquat. Sci. **63**: 1549–1563.

Bence, J.R., and Smith, K.D. 1999. An overview of recreational fisheries of the Great Lakes. *In* Great Lakes fisheries and policy management: a binational perspective. *Edited by* W.W. Taylor and C.P. Ferreri. Michigan State University Press, East Lansing, Mich. pp. 259–306.

Benoit, H.P., Johannsson, O.E., Warner, D.M., Sprules, W.G., and Rudstam, L.G. 2002. Assessing the impact of a recent predatory invader: the population dynamics, vertical distribution, and potential prey of *Cercopagis pengoi* in Lake Ontario. Limnol. Oceanogr. **47**: 626–635.

Bootsma, H.A., and Hecky, R.E. 2003. A comparative introduction to the biology and limnology of the African Great Lakes. J. Gt. Lakes Res. **29**(Suppl. 2): 3–18.

Bronte, C.R., Ebener, M.P., Schreiner, D.R., DeVault, D.S., Petzold, M.M., Jensen, D.A., Richards, C., and Lozano, S.J. 2003. Fish community change in Lake Superior, 1970–2000. Can. J. Fish. Aquat. Sci. **60**: 1552–1574.

Cohen, J.E. 1977. Ratio of prey to predators in community webs. Nature (London), **270**: 165–167.

Colautti, R.I., Bailey, S.A., van Overdijk, C.D.A., Amundsen, K., and MacIsaac, H.J. 2006. Characterised and projected costs of nonindigenous species in Canada. Biol. Invasions, **8**: 45–59.

Conroy, J.D., Kane, D.D., Dolan, D.M., Edwards, W.J., Charlton, M.N., and Culver, D.A. 2005. Temporal trends in Lake Erie plankton biomass: roles of external phosphorus loading and dreissenid mussels. J. Gt. Lakes Res. **31**(Suppl. 2): 89–110.

Dermott, R. 2001. Sudden disappearance of the amphipod *Diporeia* from eastern Lake Ontario, 1993–1995. J. Gt. Lakes Res. **27**: 423–433.

Dermott, R., and Kerec, D. 1997. Changes to the deepwater benthos of eastern Lake Erie since the invasion of *Dreissena*: 1979–1993. Can. J. Fish. Aquat. Sci. **54**: 922–930.

DeVault, D.S., Hesselberg, R., Rodgers, P.W., and Feist, T.J. 1996. Contaminant trends in lake trout and walleye from the Laurentian Great Lakes. J. Gt. Lakes Res. **22**: 884–895.

Dobiesz, N.E., McLeish, D.A., Eshenroder, R.L., Bence, J.R., Mohr, L.C., Ebener, M.P., Nalepa, T.L., Woldt, A.P., Johnson, J.E., Argyle, R.L., and Makarewicz, J.C. 2005. Ecology of the Lake Huron fish community, 1970–1999. Can. J. Fish. Aquat. Sci. **62**: 1432–1451.

Gamble, A.E., Lloyd, R., Aiken, J., Johannsson, O.E., and Mills, E.L. 2006. Using zooplankton biomass size spectra to assess ecological change in a well-studied freshwater lake ecosystem: Oneida Lake, New York. Can. J. Fish. Aquat. Sci. **63**: 2687–2699.

Hansen, M.J., and Kerr, S.R. 2004. Fish communities of the Laurentian Great Lakes: the SCOL tradition revisited for the 21st century. Great Lakes Fishery Commission Completion Report. Available from [accessed June 2006; updated July 2005].

Hecky, R.E. 1984. African lakes and their trophic efficiencies: a temporal perspective. *In* Trophic Dynamics of Aquatic ecosystems, Toronto, Ontario, January 1981. *Edited by* D.G. Meyers and J.R. Strickler. American Association for the Advancement of Science Selected Symposium 85: Trophic Interactions Within Aquatic Ecosystems. Westview Press, Inc., Boulder, Colo. pp. 405–448.

Hemmingsen, A.M. 1960. Energy metabolism as related to body size and respiratory surfaces, and its evolution. Reports of the Steno Memorial Hospital and Nordinsk Insulin Laboratorium, **9**: 6–110.

Herman, A.W. 1992. Design and calibration of a new optical plankton counter capable of sizing small zooplankton. Deep-Sea Res. Part I Oceanogr. Res. **39**: 395–415.

Johannsson, O.E. 2003. A history of changes in zooplankton community structure and function in Lake Ontario: responses to whole-lake remediation and exotic invasions. *In* State of Lake Ontario: past, present and future. *Edited by* M. Munawar. Ecovision World Monograph Series, Aquatic Ecosystem Health and Management Society, Goodword Books Pvt. Ltd., New Delhi, India. pp. 221–256.

Johannsson, O.E., Mills, E.L., and O'Gorman, R. 1991. Changes in the nearshore and offshore zooplankton communities in Lake Ontario: 1981–88. Can. J. Fish. Aquat. Sci. **48**: 1546–1557.

Johannsson, O.E., Graham, D.M., Einhouse, D.W.E., and Mills, E.L. 1999. Historical and recent changes in the Lake Erie zooplankton community and their relationship to ecosystem function. *In* State of Lake Erie: past, present and future. *Edited by* M. Munawar, T. Edsall, and I.F. Munawar. Ecovision World Monograph Series, Aquatic Ecosystem Health and Management Society, Backhuys Publishers, Leiden, The Netherlands. pp. 169–196.

Kaufman, S.D., Gunn, J.M., Morgan, G.E., and Couture, P. 2006. Muscle enzymes reveal walleye (*Sander vitreus*) are less active

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when larger prey (cisco, *Coregonus artedi*) are present. Can. J. Fish. Aquat. Sci. **63**: 970–979.

Kerr, S.R., and Dickie, L.M. 2001. The biomass spectrum: a predator–prey theory of aquatic production. Columbia University Press, New York.

Koonce, J.F., Locci, A.B., and Knight, R.L. 1999. Contributions of fishery management to changes in walleye and yellow perch populations of Lake Erie. *In* Great Lakes fisheries policy and management: a binational perspective. *Edited by* W.W. Taylor and F.C. Paola. Michigan State University Press, East Lansing, Mich. pp. 497–510.

Lehman, J.T., and Caceres, C.E. 1993. Food-web responses to species invasion by a predatory invertebrate; *Bythotrephes* in Lake Michigan. Limnol. Oceanogr. **38**: 879–891.

Loftus, K.H., and Regier, H.A. 1972. Introduction to the proceedings of the 1971 symposium on salmonid communities in oligotrophic lakes. J. Fish. Res. Board Can. **29**: 613–628.

Madenjian, C.P., Fahnenstiel, G.L., Johengen, T.H., Nalepa, T.F., Vanderploeg, H.A., Fleischer, G.W., Schneeberger, P.J., Benjamin, D.M., Smith, E.B., Bence, J.R., Rutherford, E.S., Lavis, D.S., Robertson, D.M., Jude, D.J., and Ebener, M.P. 2002. Dynamics of the Lake Michigan food web, 1970–2000. Can. J. Fish. Aquat. Sci. **59**: 736–753.

Millard, E.S., Johannsson, O.E., Neilson, M.A., and El-Shaarawi, A.H. 2003. Long-term seasonal and spatial trends in nutrients, chlorophyll *a* and light attenuation in Lake Ontario. *In* State of Lake Ontario: past, present and future. *Edited by* M. Munawar. Ecovision World Monograph Series, Aquatic Ecosystem Health and Management Society, Goodword Books Pvt. Ltd., New Delhi, India. pp. 97–132.

Mills, E.L., Casselman, J.M., Dermott, R., Fitzsimons, J.D., Gal, G., Holeck, K.T., Hoyle, J.A., Johannsson, O.E., Lantry, B.F., Makarewicz, J.C., Millard, E.S., Munawar, I.F., Munawar, M., O'Gorman, R., Owens, R.W., Rudstam, L.G., Schaner, T., and Stewart, T.J. 2003. Lake Ontario: food web dynamics in a changing ecosystem (1970–2000). Can. J. Fish. Aquat. Sci. **60**: 471–490.

Morris, T.J. 2002. Temporal and spatial patterns of zooplankton abundance and productivity in Lake Erie using an optical plankton counter. Ph.D. thesis, Department of Zoology, University of Toronto, Ont.

Negley, T.L., Mills, E.L., Baldwin, B., O'Gorman, R., and Owens, R.W. 2003. The ecology and impact of the invasion of Lake Ontario by the zebra mussel (*Dreissena polymorpha*) and quagga mussel (*D. bugensis*). *In* State of Lake Ontario: past, present and future. *Edited by* M. Munawar. Ecovision World Monograph Series, Aquatic Ecosystem Health and Management Society, Goodword Books Pvt. Ltd., New Delhi, India. pp. 559–577.

O'Neill, R.V., DeAngelis, D.L., Waide, J.B., and Allen, T.F.H. 1986. A hierarchical concept of ecosystems. Princeton University Press, Princeton, N.J.

Paloheimo, J.E., and Dickie, L.M. 1965. Food and growth of fishes 1. A growth curve derived from experimental data. J. Fish. Res. Board Can. **22**: 521–542.

Pazzia, I., Trudel, M., Ridgway, M., and Rasmussen, J.B. 2002. Influence of food web structure on the growth and bioenergetics of lake trout (*Salvelinus namaycush*). Can. J. Fish. Aquat. Sci. **59**: 1593–1605.

Pearre, S., Jr. 1986. Ratio-based trophic niche breadths of fish, the Sheldon spectrum, and the size-efficiency hypothesis. Mar. Ecol. Progr. Ser. **27**: 299–314.

Peters, R.H. 1983. The ecological implications of body size. Cambridge University Press, Cambridge, UK.

Rand, P.S., and Stewart, D.J. 1998. Dynamics of salmonine diets and foraging in Lake Ontario, 1983–1993: a test of a bioenergetic model prediction. Can. J. Fish. Aquat. Sci. **55**: 307–317.

Rand, P.S., Stewart, D.J., Lantry, B.F., Rudstam, L.G., Johannsson, O.E., Goyke, A.P., Brandt, S.B., O'Gorman, R., and Eck, G.W. 1995. Effect of lake-wide planktivory by the pelagic prey fish community in Lakes Michigan and Ontario. Can. J. Fish. Aquat. Sci. **52**: 1546–1563.

Ricciardi, A., and Atkinson, S.K. 2004. Distinctiveness magnifies the impact of biological invaders in aquatic ecosystems. Ecol. Lett. **7**: 781–784.

Rosen, R. 1991. Life itself. Columbia University Press, New York.

Ryan, P., Witzel, L.D., Paine, J.R., Freeman, M.J., Hardy, M., and Sztramko, K.L. 1999. Recent trends in Lake Erie fish stocks with a changing trophic state and food web (1980–1994). *In* State of Lake Erie: past, present and future. *Edited by* M. Munawar, T. Edsall, and I.F. Munawar. Ecovision World Monograph Series, Aquatic Ecosystem Health and Management Society, Backhuys Publishers, Leiden, The Netherlands. pp. 241–289.

Sheldon, R.W., Sutcliffe, W.H., Jr., and Paranjape, M.A. 1977. Structure of pelagic food chain and relationship between plankton and fish production. J. Fish. Res. Board Can. **34**: 2344–2353.

Sherwood, G.D., Pazzia, I., Moeser, A., Hontela, A., and Rasmussen, J.B. 2002. Shifting gears: enzymatic evidence for the energetic advantage of switching diet in wild-living fish. Can. J. Fish. Aquat. Sci. **59**: 229–241.

Sprules, W.G., and Goyke, A.P. 1994. Size-based structure and production in the pelagia of Lakes Michigan and Ontario. Can. J. Fish. Aquat. Sci. **51**: 2603–2611.

Sprules, W.G., Jin, E.H., Herman, A.W., and Stockwell, J.D. 1998. Calibration of an optical plankton counter for use in fresh water. Limnol. Oceanogr. **43**: 726–733.

Stewart, T.J., Bowlby, J.R., Rawson, M., and Eckert, T.H. 2003. The recreational boat fishery for salmonids in Lake Ontario 1985–1995. *In* State of Lake Ontario: past, present and future. *Edited by* M. Munawar. Ecovision World Monograph Series, Aquatic Ecosystem Health and Management Society, Goodword Books Pvt. Ltd., New Delhi, India. pp. 517–540.

Thiebaux, M.L., and Dickie, L.M. 1993. Structure of the body-size spectrum of biomass in aquatic ecosystems: a consequence of allometry in predator–prey interactions. Can. J. Fish. Aquat. Sci. **50**: 1308–1317.

Ulanowicz, R.E. 2003. Some steps toward a central theory of ecosystem dynamics. Comp. Biol. Chem. **27**: 523–530.

Yurista, P., Kelly, J., and Miller, S. 2005. Evaluation of optically acquired zooplankton size-spectrum data as a potential tool for assessment of condition in the Great Lakes. Environ. Manag. **35**: 34–44.

Zar, J.H. 1999. Biostatistical analysis. 4th ed. Prentice Hall, Upper Saddle River, N.J.

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Ca^{2+} handling and oxidative capacity are greatly impaired in swimming muscles of hatchery-reared versus wild Atlantic salmon (*Salmo salar*)

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Abstract: The swimming capacity of fish is strongly associated with muscle performance, although the prerequisites for effective movements have not been fully described at the molecular level. To compare the condition of swimming musculature of hatchery-reared Atlantic salmon (*Salmo salar*) with that of wild fish, we analyzed the relative level of two excitation–contraction coupling components (i.e., dihydropyridine receptor (DHPR) and ryanodine receptor (RyR)) and the oxidative capacity of muscles with histochemical and Western blot methods. The density of DHPR and RyR was considerably higher in swimming muscles of wild fingerlings (age 0+) (109.8% and 123.3% in red muscle; 128.6% and 186.0% in white muscle, respectively) and yearlings (age 1+) (153.5% and 459.1% in red muscle; 131.2% and 858.4% in white muscle) as compared with those in reared fish. Similar difference was also observed in the oxidative capacity of muscles. Moreover, the oxidative activity correlated positively with the level of DHPR and RyR. Our data indicate that calcium handling, as well as oxidative capacity of swimming muscles of reared salmon, is clearly separable from the corresponding capacities of wild fish. We suggest that the observed alteration is a major contributing factor to the well-documented differences in swimming ability between wild and hatchery-reared salmon.

Résumé : La capacité de nage des poissons est fortement reliée à la performance musculaire, bien que les conditions préalables au niveau moléculaire de mouvements efficaces n'aient pas été complètement établies. Dans notre étude, afin de comparer la condition de la musculature de nage chez des saumons atlantiques (*Salmo salar*) élevés en pisciculture et des saumons sauvages, nous analysons les niveaux relatifs de deux composantes du couplage excitation–contraction, c'est-à-dire le récepteur de la dihydropyridine (DHPR) et le récepteur de la ryanodine (RyR), ainsi que la capacité oxydative des muscles à l'aide de méthodes histochimiques et de buvardage Western. Les densités du DHPR et du RyR sont considérablement plus élevées dans les muscles de la nage des alevins sauvages (age 0+) (respectivement 109,8 % et 123,3 % dans le muscle rouge et 128,6 % et 186,0 % dans le muscle blanc) et des saumons d'un an sauvages (age 1+) (respectivement 153,5 % et 459,1 % dans le muscle rouge et 131,2 % et 858,4 % dans le muscle blanc) par comparaison aux poissons de pisciculture. Il existe aussi des différences similaires dans la capacité oxydative des muscles. De plus, il y a une corrélation positive entre l'activité oxydative et les niveaux de DHPR et de RyR. En conclusion, nos données indiquent que la gestion du calcium, de même que la capacité oxydative des muscles de nage des poissons de pisciculture, sont nettement différentes des capacités correspondantes chez les poissons sauvages. Nous croyons que l'altération que nous observons est un des facteurs importants qui expliquent les différences bien connues de capacité de nage chez les poissons sauvages et les poissons de pisciculture.

[Traduit par la Rédaction]

Introduction

Enhancement stocking programs are widely used for rehabilitation and compensation of the loss of natural reproduction of salmonids (Einum and Fleming 2001). However, it is well known that after release, reared Atlantic salmon (*Salmo salar*) do not survive in nature as well as their wild counterparts (Jonsson et al. 2003; Kallio-Nyberg et al. 2004; Jokikokko et al. 2006). There are probably multiple reasons for this difference. For instance, different behavioral patterns have been noted between reared and wild fish (Kellison et al. 2000; Brown and Laland 2001; Braithwaite and Salvanes 2005). Moreover, a hatchery provides a constant supply of food and protection from predators and enables a sustainable growing environment, allowing survival also for individuals with low fitness. Hatcheries, however, hardly prepare fish to

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survive in variable and more demanding natural environments (Olla et al. 1998). There are some ecological studies on attempting to increase stocking success. One method is to rear fish in environments mimicking the natural habitat (Braithwaite and Salvanes 2005). Training fish to avoid predation is also one of the methods used (Brown and Smith 1998; Mirza and Chivers 2000; Vilhunen and Hirvonen 2003). Despite the problem, only modest attention is paid to the performance of swimming muscles of fish; yet, prey capture and predator avoidance is directly affected by the swimming capacity.

McDonald et al. (1998) observed that by raising the water flow velocity in hatchery tanks, the endurance of Atlantic salmon was notably enhanced. Similar results in swimming capacity have also been noted in other investigations (Young and Cech 1993; Davison 1997; Holk and Lykkeboe 1998), although some uneffective results have also been observed (Kiessling et al. 1994; Gallaugher et al. 2001). Besides the differences between differentially reared salmon, McDonald et al. (1998) observed that the anaerobic capacity and swimming performance were superior in wild salmon compared with reared ones. Moreover, the oxygen carrying capacity and the capacity to osmoregulate in seawater are found to be surpassing in wild salmon smolts (Virtanen 1988). Despite the observed physiological differences between wild and reared fish, there are no investigations concerning the excitation–contraction (EC) coupling mechanism of swimming muscles, although the EC coupling ultimately regulates the contraction of muscles (Lamb 2000; Fill and Copello 2002).

The muscle contraction is initiated by a rise in the concentration of intracellular Ca^{2+} ions in muscle fiber caused by EC coupling machinery. Dihydropyridine receptors (DHPRs) and ryanodine receptors (RyRs) are the two main components of EC coupling mechanism (Lamb 2000; Fill and Copello 2002). In fish, however, the exact mechanism of Ca^{2+} release is still unclear. It has been proposed that EC coupling could occur by two different mechanisms (O'Brien et al. 1995; Fill and Copello 2002). In both events, DHPRs are activated by depolarization of T tubules. As a consequence of activation, the conformation of DHPRs changes, resulting in opening of RyRs by mechanical interaction. On the other hand, the activation could also open DHPRs acting as calcium channels, which lead to inflow of Ca^{2+} from the extracellular space into the fiber. This inflow achieves Ca^{2+}-induced Ca^{2+} release from the sarcoplasmic reticulum via RyRs (Lamb 2000; Fill and Copello 2002).

In addition to the important role triggering contraction of muscle, the amount of DHPRs has been shown to be in direct relationship to power capacity of muscles. In mammals, it has been shown that both velocity and force of the contraction increase as a consequence of enhanced DHPR level (Kandarian et al. 1992; Golden et al. 2003; Mänttäri and Järvilehto 2005). Since the receptors are essential for muscle function, the relative level of both receptors in swimming muscles of wild and hatchery-reared Atlantic salmon is compared in this study. Moreover, activity of the oxidative enzyme succinate dehydrogenase (SDH) is compared between the fish groups to specify the differences in the aerobic capacity in muscles of wild and reared salmon. In addition, the levels of DHPRs and RyRs are compared with the oxidative activity of muscles.

Materials and methods

This study was carried out in autumn 2005 at the Game and Fishery Research Institute at Paltamo, Finland. Fingerlings (age 0+) and yearlings (age 1+) of Atlantic salmon from River Simojoki brood stock of wild origin from the first generation were reared in standard cultivation tanks with a density of 10 000 per tank with a bottom surface area of 3.5 m^2 and depth of 23 cm and 5000 per tank with a bottom surface area of 15.0 m^2 and depth of 50 cm, respectively. The natural water temperature and photoperiod was maintained. Fish were fed three times a day with commercial fish pellets (Bio-Optimal C80, Bio-Mar, Finland). The food was offered to the point at which the fish stopped eating. Catching the fish was performed by netting from the tanks with lowered water depth to ensure equal catching probability. Wild salmon from the same age groups were obtained by electrofishing from the River Simojoki (65°38 N, 25°00 E). The age of fish were verified from scale samples. The water flow velocity was measured from the area of the tank that fish preferred and from the exact same points of the river where fish were caught. The experiment protocol was approved by the Animal Ethics Committee of the University of Oulu (license No. 083/04).

Fluorescence labeling

Eight salmon from each group were killed by decapitation. Total lengths and weights of the salmon were measured to calculate Fulton's condition factor (CF = [weight (g) · length^{-3} (cm)] × 100). After the measurements, the fish were frozen with liquid nitrogen and stored in –80 °C. Blocks of muscles were obtained caudally from the adipose fin and cut into 14 µm cross-sections with a cryostat microtome at –20 °C. The sections were incubated in high-affinity enantiomer of dihydropyridine (20 nmol·L^{-1}) and ryanodine (0.5 µmol·L^{-1}) (ST-BODIPY®, Molecular Propes, Netherlands) solutions for 90 min and processed as previously described in Mänttäri et al. (2001). The control samples were prepared according to Larsson et al. (1998) by preincubating the sections with cold, nonfluorescing DHP (nifedipine) or Ry (dandrolene) blockers. The images of the sections were obtained with confocal laser scanning microscope (LSM-5 Pascal, Zeiss, Germany) by using excitation at 543 nm for DHPR and 488 nm for RyR. The relative level of receptors was measured by analyzing the fluorescence intensity in the sections (LSM 5 PASCAL software 3.2, Zeiss, Germany).

Oxidative capacity

To measure the oxidative capacity of muscles, one additional set of cross-sections was processed simultaneously for SDH activity (Nachlas et al. 1957). The sections were scanned with a confocal microscope. The average intensity of staining was measured with LSM 5 PASCAL software 3.2 (Zeiss, Germany).

Western blotting

Since the sequence of the DHPR has been analyzed only for the white muscle (Grabner et al. 1991), the red muscles were not treated with Western blotting method. White muscle samples from each salmon were taken anteriorly from

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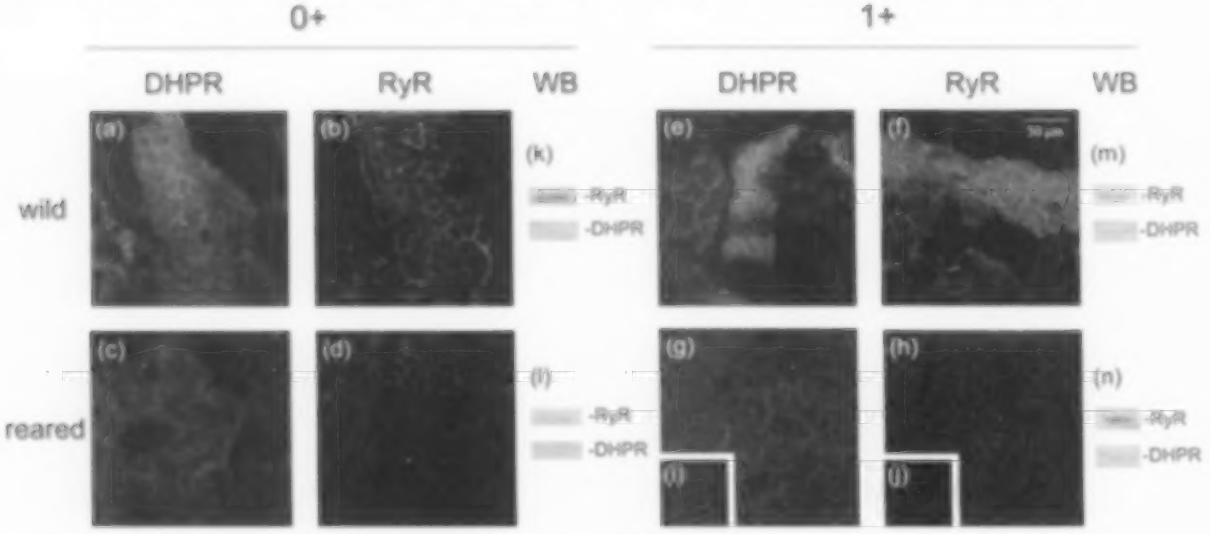
Fig. 1. Sections from muscles of wild (*a*, *b*) and reared (*c*, *d*) fingerlings (0+) and wild (*e*, *f*) and reared (*g*, *h*) yearlings (1+) of Atlantic salmon (*Salmo salar*). Relative levels of dihydropyridine receptor (DHPR) (*a*, *c*, *e*, *g*) and ryanodine receptor (RyR) (*b*, *d*, *f*, *h*) was investigated by incubating muscle sections in 20 nmol·L^{-1} high-affinity enantiomer of DHP labeled with orange fluorophore and 0.5 μmol·L^{-1} high-affinity enantiomer of Ry labeled with green fluorophore. Inserts show control samples preincubated with nifedipine (*i*) or dantrolene (*j*). The corresponding membranes containing electrophoretically separated DHPRs and RyRs as treated with Western blotting (WB) method are presented besides section figures (wild fingerlings (*k*), reared fingerlings (*l*), wild yearlings (*m*), reared yearlings (*n*)).



the adipose fin. The samples were homogenized in 6 volumes of homogenization buffer (62.5 mmol·L^{-1} Tris–HCl, pH 6.8). The protein concentration was assayed as described in Bradford (1976). The homogenized samples were denatured in sample buffer according to Laemmli (1970) for 7 min at 70 °C. Aliquots of total protein extract (24 μg) were analyzed by electrophoresis on 7.5% polyacrylamide sodium dodecyl sulphate (SDS) gels and blotted onto nitrocellulose membrane (Bio-Rad, USA) as previously described in Towbin et al. (1979). Western immunodetection of proteins was performed in Tris-buffered saline plus Tween 20 (0.05%). The blots were first incubated with primary antibody (DHPR α1S, 1:250, Santa Cruz Biotechnology Inc., USA; monoclonal anti-ryanodine receptor clone 34 C, 1:4000, Sigma-Aldrich Inc., USA) for 2 h, then with secondary antibody (blotting grade affinity purified goat anti-mouse IgG H+L alkaline phosphatase conjugate, 1:3000, Bio-Rad, USA) also for 2 h. The proteins were visualized using bromo-4-chloro-3-indolyl phosphate mono-(-toluidinium) salt – nitro blue tetrazolium (BCIP–NBT) substrate. The optical densities of the detected bands were analyzed with the FluorS MultiImager program (Bio-Rad, USA).

Statistical analysis

The values are presented as means ± standard error (SE). The difference in the relative level of receptors and SDH activity in swimming muscles between wild and reared salmon was analyzed with independent *t* tests. The correlation between the levels of DHPR and RyR and SDH activity in muscle sections was evaluated with Spearman's correlation test. The statistical analyses were performed with the R 2.2.1 for Windows software (The R Project for Statistical Computing, www.r-project.org).

Results

To evaluate the swimming velocities of salmon, water flow velocities in different habitats were measured. The velocities (body lengths per second) were 5.36 ± 0.22 (wild, 0+), 3.16 ± 0.06 (wild, 1+), 0.82 ± 0.03 (reared, 0+), and 0.66 ± 0.03 (reared, 1+). The overall condition of wild and reared fingerlings and yearlings was compared by calculating the Fulton's CF values. CFs of wild fingerlings and yearlings were 0.805 ± 0.022 and 0.811 ± 0.009, respectively. For the respective reared salmon, the variables were 0.877 ± 0.025 and 0.989 ± 0.023. CFs of wild and reared salmon differed significantly from each other (fingerlings: $p = 0.05$; and yearlings: $p = 5.00 \times 10^{-5}$). Wild fish were also significantly smaller than reared ones. The average length and weight of the fingerlings were 5.3 ± 0.21 cm and 1.3 ± 0.16 g (wild) and 7.4 ± 0.30 cm and 3.7 ± 0.52 g (reared) ($p = 8.3 \times 10^{-5}$ and $p = 0.002$ for lengths and weights, respectively). Respective values of the yearlings were 8.9 ± 0.16 cm and 5.7 ± 0.31 g (wild) and 17.5 ± 0.73 cm and 55.7 ± 7.53 g (reared) ($p = 3.8 \times 10^{-6}$ and $p = 0.0003$).

To analyze the relative levels of DHPR and RyR in swimming muscles of salmon, both fluorescence labeling and Western blotting methods were used. In both age groups the relative level of receptors was significantly lower in swimming muscles of reared salmon as analyzed by fluorescence labeling (Fig. 1). In red muscle of wild fingerlings, the relative level of DHPR was 109.8% ($p = 5.41 \times 10^{-6}$) and that of RyR was 123.3% ($p = 0.00083$) higher compared with red muscle from reared salmon. In white muscle, the corresponding values were 128.6% ($p = 3.83 \times 10^{-5}$) and 186.0% ($p = 0.0011$). In wild yearlings, the relative levels of DHPR and RyR in red muscle were 153.5% ($p = 2.59 \times 10^{-5}$) and

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Table 1. Relative level of dihydropyridine receptors (DHPRs) and ryanodine receptors (RyRs) in red and white muscles of wild and reared fingerling (age 0+) and yearling (age 1+) Atlantic salmon (*Salmo salar*) as analyzed with fluorescence labeling (fluor) and Western blotting (WB) methods.

	Age 0+		Age 1+	
	Wild	Reared	Wild	Reared
DHPR, fluor, red muscle	55.1±2.81 ***	26.3±2.93	52.8±3.96 ***	20.8±3.25
RyR, fluor, red muscle	35.3±3.74 ***	15.8±1.81	33.9±3.95 ***	6.1±1.02
DHPR, fluor, white muscle	27.0±1.94 ***	11.8±0.83	20.8±0.72 ***	9.0±1.66
RyR, fluor, white muscle	26.6±3.38 **	9.3±1.11	22.8±3.76 ***	2.4±0.59
DHPR, WB, white muscle	2.1±0.28 *	1.2±0.25	2.2±0.30	2.9±0.32
RyR, WB, white muscle	5.4±0.52 **	2.8±0.39	4.9±0.64 **	11.0±1.31
SDH, red muscle	14.7±0.70 ***	2.2±0.14	18.5±0.88 ***	1.9±0.09
SDH, white muscle	0.9±0.09 **	0.5±0.04	1.1±0.06 ***	0.6±0.06

Note: The values are mean intensities ± standard error (SE). The activity of succinate dehydrogenase (SDH) are presented as (1/light intensity) × 1000. Significant differences between wild and reared group are shown: ***, $p < 0.001$; **, $p < 0.01$; *, $p < 0.05$.

459.1% ($p = 0.00014$) higher, respectively, compared with that in reared fish. Similar results were seen in white muscle sections: DHPR = 131.2% ($p = 8.07 \times 10^{-5}$) and RyR = 858.4% ($p = 0.00089$). Some of the receptor levels changed as a function of age of the fish. In reared salmon, the level of RyR decreased with the age as analyzed with the fluorescence labeling method ($p = 0.00066$ in red muscle and $p = 0.00020$ in white muscle). The Western blotting method showed enhanced levels of RyR ($p = 0.00084$) and DHPR ($p = 0.0016$) in the white muscle of reared yearlings as compared with levels in the muscles of reared fingerlings. In the white muscle of wild fingerlings, the level of DHPR was higher ($p = 0.015$) than that in wild yearlings as analyzed from fluorescence sections. Results obtained with Western blotting for white muscle from 1+ reared fish were parallel to that obtained with fluorescence analysis. In the fingerlings, both methods showed a higher level of receptors in the wild salmon as compared with levels in the reared ones (all results are presented in Table 1).

The activity of SDH was analyzed from muscle sections to compare the oxidative capacity of muscles of wild and reared salmon. The staining was 570.2% ($p = 2.04 \times 10^{-7}$) higher in red muscle and 72.1% ($p = 0.0043$) higher in white muscle of wild fingerlings compared with the staining in the sections from reared fish. In yearlings, the corresponding values were 889.8% ($p = 2.25 \times 10^{-7}$) and 87.4% ($p = 1.11 \times 10^{-5}$). The activity of SDH was higher in the red muscle of wild yearlings as compared with the wild fingerlings ($p = 0.0042$). The staining intensity of SDH correlated positively with the relative levels of both DHPR and RyR in both red and white muscle as analyzed from the fluorescence labeling sections. The Spearman's rho value between DHPR level and SDH activity was 0.735 ($p = 1.65 \times 10^{-6}$) in red muscle and 0.533 ($p = 0.0017$) in white muscle. The rho value between RyR level and SDH activity in red muscle was 0.763 ($p = 3.90 \times 10^{-7}$) and in white muscle 0.524 ($p = 0.0021$).

Discussion

This study demonstrates for the first time that the relative levels of DHPR and RyR are significantly lower in the swimming muscles of reared salmon as compared with that of wild fish. A similar difference is clearly seen in the oxidative capacity of muscles. Moreover, the oxidative activity correlated positively with the levels of DHPR and RyR.

DHPRs and RyRs are a crucial part of muscle function regulating the contraction of muscles (Lamb 2000; Fill and Copello 2002). Furthermore, the relative level of receptors affects directly the force and velocity of muscle contraction (Kandarian et al. 1992; Golden et al. 2003; Mänttäri and Järvilehto 2005). Based on these observations, it seems that the overall power capacity of muscles of wild salmon is superior compared with the muscle performance of reared salmon. Moreover, higher oxidative capacity of muscles enables ability for longer-lasting, continuous swimming events (Johnston 1980).

The results from fluorescence labeling and Western blotting methods were quite dissimilar for white muscle of reared yearlings. In previous investigations, red and white muscle of fish has been observed to contain multiple RyR isoforms (Franck et al. 1998; Morrissette et al. 2000; Fill and Copello 2002). In fish, DHPRs have only been investigated in white muscles (Grabner et al. 1991). In mammals, however, skeletal muscles also express several DHPR isoforms (Fill and Copello 2002). Considering this, wild and reared salmon could express differential ratios of different isoforms. Moreover, this could be influenced by age. Different isoforms could thus explain the dissimilar results from fluorescence labeling and Western blotting methods, since in the Western blotting method, antibodies identify only receptors with special sequence, while in the fluorescence labeling method, Ry or DHP binds equally to every isoform.

The differences in the density of receptors between reared and wild fish, as revealed by fluorescent labeling in both age groups and by Western blotting in fingerlings, could be explained by water flow velocity. The flow velocity in the river habitat was at least 6.5 times higher compared with stocking tank. In a previous study (Mänttäri et al. 2005), it was shown that active downstream migration associated with increased swimming activity enhanced the relative level of DHPRs in both red and white muscles of salmon smolts as analyzed with the fluorescence labeling method. Moreover, training increases the level of receptors in skeletal muscles of both fish and mammals (Saborido et al. 1995; Ørtenblad et al.

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2000; Anttila et al. 2006). Therefore, it seems that swimming velocity could be one factor affecting the relative level of receptors. Furthermore, it has been shown that in nature, fish encounter a more challenging environment, including avoidance of predators and catching prey (Olla et al. 1998; Brown and Laland 2001). Both events require high swimming capacity, which could be achieved with high density of DHPRs and RyRs. On the other hand, in rearing tanks, fish encounter a constant water flow, while the flow in nature is more turbulent. Thus, it seems that burst-type swimming enhances the level of receptors more efficiently than endurance swimming. Strength-type swimming requires high power capacity from the muscles, which could be achieved with the higher levels of DHPR and RyR. However, a more demanding natural environment had an impact on the size and the condition factor of salmon; these were lower in wild fish. In nature, fish are forced to consume energy for pure survival, while salmon reared in hatcheries have a high energy intake in combination with low energy demand, resulting in a higher condition factor.

The age of the fish did not have a major impact on the level of receptors or the oxidative capacity of muscles. However, the level of RyR was lower in the reared yearlings compared with the fingerlings as analyzed from the fluorescence sections. There could be some isoform alterations with age, since the amount of receptors increased when analyzed from the Western blots. The SDH activity, on the other hand, increased in wild yearlings as compared with fingerlings, but the change was minor (25.9%). In previous investigations, it has been shown that muscle performance increases during development (Proctor et al. 1980; Fisher et al. 2000; Müller and van Leeuwen 2004). However, in these studies the fish were in the early stage of the development, whereas in the present investigation the fingerlings were about 4–5 months old. It seems that at least in wild fish, muscle contraction capacity had developed by that age. One of the factors that could affect the results between wild and reared fish is the size of the fish. At the rearing station, food was offered up to the stage where the fish stopped eating. The unlimited food resource may enable the maximum growing velocity of reared fish. It has not, however, been shown whether the contraction machinery of muscles develops simultaneously with rapidly growing muscle fibers. The bigger size of reared fish could thus affect the lower level of RyRs and DHPRs as well as the oxidative capacity in the muscles of reared salmon.

The swimming performance of wild fish is superior to that of reared ones according to McDonald et al. (1998). On the other hand, training involving enhanced swimming activity has also been shown to increase the swimming capacity of fish (Young and Cech 1993; Davison 1997; Holk and Lykkeboe 1998), although some dissimilar results have been observed as well (Kiessling et al. 1994; Gallaugher et al. 2001). In the studies of Kiessling et al. (1994) and Gallaugher et al. (2001), the oxygen carrying capacity and the amount of total body protein increased after training, indicating improved fitness due to training. However, the effect of training on the swimming capacity of fish is hard to compare between species, since, for example, swimming patterns differ between the fish species used in previous investigations; however, the results of the present study do support the conclusion that swimming activity might affect the performance of muscles. On the other hand, domestication is a factor that might also have an effect on the results obtained. In previous studies, it has been speculated that domestication could lead to lower swimming capacity of fish (Enders et al. 2004). In the present study, the fish were kept in captivity only for one generation, and the effect of domestication was thus unsubstantial. The density of fish in the rearing tank has also been shown to affect the metabolism of muscles (McDonald et al. 1998). In this investigation, the density of reared fish was quite high and could thus influence the results. Despite the density differences, natural selection pressure in the wild is more pronounced compared with the rearing tanks, and in the wild only highly fit individuals survive. This could be the ultimate reason for the differences between wild and reared salmon observed in present study.

The considerably lower muscle metabolism of reared salmon was seen especially in the activity of SDH in the muscle sections. First, the oxidative activity in both red and white muscles of wild fish was superior to that in reared ones. Second, the oxidative activity in reared fish was not remarkably higher in the red muscles compared with that in white muscles (in fingerling the difference between red and white muscle was 340% and in yearlings 217%). One reason for this could be a decreased amount or diminished activity of mitochondria in the red muscle of reared salmon. Further investigations should be made to address these questions. However, it is certain that both declined oxidative activity and the lower level of EC coupling components affect muscle performance in reared salmon.

Throughout the world, numerous stocking programs have been established to maintain commercially viable populations of fish (Welcomme and Bartley 1998). However, the mortality level of reared fish is dramatic. For example, around 5 billion hatchery-reared salmon are released worldwide annually, but only less than 5% survive to reproducing age (McNeil 1991). During the 1990s, the survival declined further, to around 0.2%–2.9% in the area of the North Atlantic (Jonsson et al. 2003). The protected growing environment of reared salmon may play a role in the poor survival because of low selection pressure in the hatcheries. In reared fish, the selection occurs after the releasing, which lowers the survival rate of reared fish. There are several ongoing investigations attempting to enhance the stocking success. Social learning and life skills training constitute one part of these investigations (Brown and Laland 2001). The aspect behind these investigations is the poor feeding strategies and avoidance of predators of reared fish (Ellis et al. 2002; Olla et al. 1994, 1998). However, these investigations do not take into account the swimming capacity of fish. Even though the behavior of the fish may become more natural, the swimming capacity to escape predators, for example, remains the same. The present study indicates that wild salmon have higher Ca^{2+} handling and oxidative capacity in their muscles, and one reason behind these differences could be the more active use of muscles. The levels of DHPR and RyR, as well as oxidative capacity, could, however, be increased by training the salmon in hatchery tanks (Anttila et al. 2006). Moreover, it has been shown that training reduces stress responses in fish, which could also enhance the sur-

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vival of reared fish (Woodward and Smith 1985; Young and Cech 1993; Hernandez et al. 2002).

In conclusion, both Ca^{2+} handling and oxidative capacity of swimming muscles of wild salmon are superior compared with reared ones. More active use of muscles in wild salmon could be one reason for these findings. It seems that in the future, the stocking success of reared fish could be enhanced by training both (*i*) the swimming capacity and (*ii*) the life skill strategies of fish before release to nature. However, neither of these strategies eliminates the weak individuals from the population.

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References

Anttila, K., Mänttäri, S., and Järvilehto, M. 2006. Effects of different training protocols on Ca^{2+} handling and oxidative capacity in skeletal muscle of Atlantic salmon (*Salmo salar* L.). J. Exp. Biol. **209**: 2971–2978.

Bradford, M. 1976. A rapid and sensitive method for the quantitation of microgram quantities of protein utilizing the principle of protein–dye binding. Anal. Biochem. **72**: 248–254.

Braithwaite, V.A., and Salvanes, A.G. 2005. Environmental variability in the early rearing environment generates behaviourally flexible cod: implications for rehabilitating wild populations. Proc. R. Soc. Lond. B Biol. Sci. **272**: 1107–1113.

Brown, C., and Laland, K. 2001. Social learning and life skills training for hatchery reared fish. J. Fish Biol. **59**: 471–493.

Brown, G.E., and Smith, R.J.F. 1998. Acquired predator recognition in juvenile rainbow trout (*Oncorhynchus mykiss*): conditioning hatchery-reared fish to recognize chemical cues of a predator. Can. J. Fish. Aquat. Sci. **55**: 611–617.

Davison, W. 1997. The effects of exercise training on teleost fish, a review of recent literature. Comp. Biochem. Physiol. A, **117**: 67–75.

Einum, S., and Fleming, I.A. 2001. Implications of stocking: ecological interactions between wild and released salmonids. Nord. J. Freshw. Res. **75**: 56–70.

Ellis, T., Hughes, R.N., and Howell, B.R. 2002. Artificial dietary regime may impair subsequent foraging behaviour of hatchery-reared turbot released into natural environment. J. Fish Biol. **61**: 252–264.

Enders, E.C., Boisclair, D., and Roy, A.G. 2004. Differences in the energetic cost of swimming in turbulent flow between wild, farmed and domesticated juvenile Atlantic salmon *Salmo salar*. J. Fish Biol. **65**: 317.

Fill, M., and Copello, J.A. 2002. Ryanodine receptor calcium release channels. Physiol. Rev. **82**: 893–922.

Fisher, R., Bellwood, D.R., and Job, S.D. 2000. Development of swimming abilities in reef fish larvae. Mar. Ecol. Prog. Ser. **202**: 163–173.

Franck, J.P.C., Morrissette, J., Keen, J.E., Londraville, R.L., Beamsley, M., and Block, B.A. 1998. Cloning and characterization of fiber type-specific ryanodine receptor isoforms in skeletal muscles of fish. Am. J. Physiol. C, **275**: 401–415.

Gallaugher, P.E., Thorarensen, H., Kiessling, A., and Farrell, A.P. 2001. Effect of high intensity exercise training on cardiovascular function, oxygen uptake, internal oxygen transport and osmotic balance in Chinook salmon (*Oncorhynchus tshawytscha*) during critical speed swimming. J. Exp. Biol. **204**: 2861–2872.

Golden, K.L., Marsh, J.D., Jiang, Y., Brown, T., and Moulden, J. 2003. Gonadectomy of adult male rats reduces contractility of isolated cardiac myocytes. Am. J. Physiol. **285**: E449–E453.

Grabner, M., Friedrich, K., Knaus, H.-G., Striessnig, J., Scheffauer, F., Staudinger, R., Koch, W.J., Schwartz, A., and Glossmann, H. 1991. Calcium channels from *Cyprinus carpio* skeletal muscle. Proc. Natl. Acad. Sci. U.S.A. **88**: 727–731.

Hernandez, M.D., Mendiola, P., de Costa, J., and Zamora, S. 2002. Effects of intense exercise training on rainbow trout growth, body composition and metabolic responses. J. Physiol. Biochem. **58**: 1–7.

Holk, K., and Lykkeboe, G. 1998. The impact of endurance training on arterial plasma K^+ levels and swimming performance of rainbow trout. J. Exp. Biol. **201**: 1373–1380.

Johnston, I.A. 1980. Specialization of fish muscle. *In* Development and specialization of skeletal muscle. *Edited by* D.F. Goldspink. Cambridge University Press, New York. pp. 123–148.

Jokikokko, E., Kallio-Nyberg, I., Saloniemi, I., and Jutila, E. 2006. The survival of semi-wild, wild and hatchery-reared Atlantic salmon smolts of the Simojoki River in the Baltic Sea. J. Fish Biol. **68**: 430–442.

Jonsson, N., Jonsson, B., and Hansen, L.P. 2003. The marine survival and growth of wild and hatchery-reared Atlantic salmon. J. Appl. Ecol. **40**: 900–911.

Kallio-Nyberg, I., Jutila, E., Saloniemi, I., and Jokikokko, E. 2004. Associations between environmental factors, smolt size and the survival of wild and reared Atlantic salmon from the Simojoki River in the Baltic Sea. J. Fish Biol. **65**: 122–134.

Kandarian, S., O'Brien, S., Thomas, K., Schulte, L., and Navarro, J. 1992. Regulation of skeletal muscle dihydropyridine receptor gene expression by biomechanical unloading. J. Appl. Physiol. **72**: 2510–2514.

Kellison, G.T., Eggleston, D.B., and Burke, J.S. 2000. Comparative behaviour and survival of hatchery-reared versus wild summer flounder (*Paralichthys dentatus*). Can. J. Fish. Aquat. Sci. **57**: 1870–1877.

Kiessling, A., Higgs, D.A., Eales, J.G., and Dosanjh, B.S. 1994. Influence of sustained exercise and ration level on the performance of Chinook salmon (*Oncorhynchus tshawytscha* Walbaum) in seawater. Can. J. Fish. Aquat. Sci. **51**: 1975–1984.

Laemmli, U.K. 1970. Cleavage of structural proteins during assembly of head of bacteriophage T4. Nature (London), **227**: 680–685.

Lamb, G.D. 2000. Excitation–contraction coupling in skeletal muscle: comparison with cardiac muscle. Clin. Exp. Pharmacol. Physiol. **27**: 216–224.

Larsson, D., Lundgren, T., and Sundell, K. 1998. Ca^{2+} uptake through voltage-gated L-type Ca^{2+} channels by polarized enterocytes from Atlantic cod *Gadus morhua*. J. Membr. Biol. **164**: 229–237.

McDonald, D.G., Milligan, C.L., McFarlane, W.J., Croke, S., Currie, S., Hooke, B., Angus, R.B., Tufts, B.L., and Davidson, K. 1998. Condition and performance of juvenile Atlantic salmon (*Salmo salar*): effects of rearing practices on hatchery fish and comparison with wild fish. Can. J. Fish. Aquat. Sci. **55**: 1208–1219.

McNeil, W.J. 1991. Expansion of cultured Pacific salmon into marine ecosystems. Aquaculture, **98**: 173–183.

Mirza, R.S., and Chivers, D.P. 2000. Predator-recognition training enhances survival of brook trout: evidence from laboratory and field-enclosure studies. Can. J. Zool. **78**: 2198–2208.

Morrissette, J., Xu, L., Nelson, A., Meissner, G., and Block, B.A. 2000. Characterization of RyR1-slow, a ryanodine receptor specific to slow-twitch skeletal muscle. Am. J. Physiol. **279**: R1889–R1898.

© 2007 NRC Canada

Müller, U.K., and van Leeuwen, J.L. 2004. Swimming of larval zebrafish: ontogeny of body waves and implications for locomotory development. J. Exp. Biol. **207**: 853–868.

Mänttäri, S., and Järvilehto, M. 2005. Comparative analysis of mouse skeletal muscle fibre type composition and contractile responses to calcium channel blocker. BMC Physiol. **5**: 4.

Mänttäri, S., Pyörnilä, A., Harjula, R., and Järvilehto, M. 2001. Expression of L-type calcium channels associated with postnatal development of skeletal muscle function in mouse. J. Muscle Res. Cell Mot. **22**: 61–67.

Mänttäri, S., Anttila, K., and Järvilehto, M. 2005. Effects of downstream migration on myosin heavy chain expression and dihydropyridine receptor density in farmed smolt of Atlantic salmon. J. Fish Biol. **66**: 1437–1446.

Nachlas, M.M., Tsou, K., De Saiza, E., Cheng, C., and Seligman, A. 1957. Cytochemical demonstration of succinic dehydrogenase by the use of new p-nitrophynyl substituted ditetrazole. J. Histochem. Cytochem. **3**: 170–195.

O'Brien, J., Valdivia, H.H., and Block, B.A. 1995. Physiological differences between the alpha and beta ryanodine receptors of fish skeletal muscle. Biophys. J. **68**: 471–482.

Olla, B.L., Davis, M.W., and Ryer, C.H. 1994. Behavioural deficits in hatchery-reared fish: potential effects on survival following release. Aquat. Fish. Manag. **25**: 19–34.

Olla, B.L., Davis, M.W., and Ryer, C.H. 1998. Understanding how the hatchery environment represses or promotes the development of behavioural survival skills. Bull. Mar. Sci. **62**: 531–550.

Ortenblad, N., Lunde, P.K., Levin, K., Andersen, J.L., and Pedersen, P.K. 2000. Enhanced sarcoplasmic reticulum Ca^{2+} release following intermittent sprint training. Am. J. Physiol. **279**: R152–R160.

Proctor, C., Mosse, P.R.L., and Hudson, R.C.L. 1980. A histochemical and ultrastructural study of the development of the propulsive musculature of the brown trout, *Salmo trutta* L., in relation to its swimming behaviour. J. Fish Biol. **16**: 309–329.

Saborido, A., Molano, F., Moro, G., and Megías, A. 1995. Regulation of dihydropyridine receptor levels in skeletal and cardiac muscle by exercise training. Pflügers Arch. **429**: 364–369.

Towbin, H., Staehelin, T., and Gordon, J. 1979. Electrophoretic transfer of proteins from polyacrylamide gels to nitrocellulose sheets: procedure and some applications. Proc. Natl. Acad. Sci. U.S.A. **76**: 4350–4354.

Vilhunen, S., and Hirvonen, H. 2003. Innate antipredator responses of Arctic char (*Salvelinus alpinus*) depend on predator species and their diet. Behav. Ecol. Sociobiol. **55**: 1–10.

Virtanen, E. 1988. Smolting and osmoregulation of Baltic salmon *Salmo salar* L., in fresh and brackish water. Ph.D. thesis, Department of Zoology, University of Helsinki, Finland.

Welcomme, R.L., and Bartley, D.M. 1998. An evaluation of present techniques for the enhancement of fisheries. FAO, Rome, Italy. FAO Fish. Tech. Pap. 374.

Woodward, J.J., and Smith, L.S. 1985. Exercise training and stress response in rainbow trout, *Salmo gairdneri* Richardson. J. Fish Biol. **26**: 435–447.

Young, P.S., and Cech, J.J. 1993. Improved growth, swimming performance, and muscle development in exercise-conditioned young-of-the-year striped bass (*Morone saxatilis*). Can. J. Fish. Aquat. Sci. **50**: 703–707.

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A statistical modeling method for estimating mortality and abundance of spawning salmon from a time series of counts

R. Glenn Szerlong and David E. Rundio

Abstract: We present a statistical modeling method for estimating mortality and abundance of spawning salmon from time-series counts that eliminates the need for separate information about mortality. We model arrival and mortality using differential equations, where mortality can be constant or changing linearly, and estimate mortality and abundance from counts using maximum likelihood when multiple estimates of detection rate are available. We also develop an approximate likelihood to estimate mortality and abundance when only a single value for detection rate is available or to estimate only mortality when detection rates are entirely unknown. We demonstrate our approach using counts of coho salmon (*Oncorhynchus kisutch*) where mortality, abundance, and detection were determined from tagging at a weir. Our model for nonconstant mortality produced mortality estimates that closely matched the empirical data and were robust to variation in other parameters. It also provided a better fit to the stream counts and a closer abundance estimate to the weir count than the constant mortality model. Monte Carlo simulations indicated that the approximate likelihood provided reasonable estimates of mortality over most of the ranges of parameters explored, particularly under the nonconstant mortality model, and produced relatively unbiased abundance estimates using a single value for detection.

Résumé : Nous présentons une méthode de modélisation statistique pour estimer la mortalité et l'abondance de saumons en fraie à partir de séries chronologiques de dénombrements sans nécessiter de renseignements séparés sur la mortalité. Nous modélisons l'arrivée et la mortalité à l'aide d'équations différentielles dans lesquelles la mortalité peut être constante ou changer de façon linéaire et nous estimons la mortalité et l'abondance d'après les dénombrements en utilisant une méthode de vraisemblance maximale lorsqu'il existe des estimations multiples du taux de détection. Nous avons aussi mis au point une vraisemblance approximative pour estimer la mortalité et l'abondance lorsqu'une seule valeur du taux de détection est connue ou alors pour estimer la mortalité seule lorsque le taux de détection est complètement inconnu. Nous illustrons notre méthodologie en déterminant la mortalité, l'abondance et la détection chez des saumons coho (*Oncorhynchus kisutch*) à l'aide de dénombrements obtenus par marquage à un barrage. Notre modèle à mortalité non constante produit des estimations de la mortalité qui correspondent de près aux valeurs empiriques et qui sont robustes en cas de variation des autres variables. Ce modèle produit aussi un meilleur ajustement aux dénombrements dans le cours d'eau et une estimation plus exacte de l'abondance à partir des dénombrements au barrage que le modèle à mortalité constante. Des simulations de Monte Carlo indiquent que la vraisemblance approximative permet de faire des estimations adéquates de la mortalité sur presque toute l'étendue des variables examinées, particulièrement avec le modèle à mortalité non constante; elle génère des estimations relativement peu faussées de l'abondance lorsqu'on utilise une seule valeur de détection.

[Traduit par la Rédaction]

Introduction

The "area under the curve" (AUC) method is a common technique for estimating abundance of spawning salmon in streams and rivers (Neilson and Geen 1981; English et al. 1992; Irvine et al. 1992). By this method, counts of live fish made during periodic surveys are converted to an estimate of total abundance by fitting a curve to the entire time series of counts (usually after adjusting the counts for detection rates less than one), integrating the curve numerically to calculate a total number of fish-days, and then dividing this total fish-days by the mean individual survival time in days. This method, while conceptually simple, has several limitations in practice. First, in addition to the time-series counts, it requires data on detection and survival rates that often are difficult to obtain. Second, because the method is essentially

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deterministic, there is no clear way to account for missing counts or to include uncertainty of detection and survival estimation in the final abundance estimate.

New statistical modeling approaches have been developed recently that address some of the limitations of traditional AUC methods to improve accuracy, estimate uncertainty, and permit estimation with fewer data. Quinn and Gates (1997) developed a general likelihood approach for estimating escapement of pink salmon (*Oncorhynchus gorbuscha*) by treating spawner abundance as an unknown but estimable function of a stochastic arrival-and-death model. Various functions for the immigration and mortality dynamics then can be fitted to the data by, for example, maximum likelihood (ML), and the resulting abundance estimates compared for accuracy against the observed time-series counts. Errors of estimation, where they occur, might be thought of as arising either from unpredictable variability in the random immigration and mortality components of the model or else as a consequence of imperfect sampling. The decided-upon error structure of the data thus implies a particular likelihood model, which (if sufficient information is available for likelihood maximization) then serves as a basis for estimating missing counts, estimating precision, and selecting among sets of possibly competing arrival or death models.

The major limitation of the method of Quinn and Gates (1997) is that extensive data on immigration and mortality dynamics are required to fit the model, and several adaptations of their general approach have been developed subsequently for situations in which these data are limited or unavailable. The most common approach ties a parametric function for arrival times and auxiliary data on mean mortality into likelihood models for sampling errors. For example, Hilborn et al. (1999) reduced the need for additional time-series data on arrival and mortality by modeling temporal autocorrelation in abundance counts by a probability density curve and by constraining the expected number of deaths to depend on the time of peak abundance and the mean survival time (i.e., longevity) of spawners (for an extension to steelhead (*Oncorhynchus mykiss*), see Korman et al. 2002). Estimates of longevity are obtained from prior or auxiliary data (in these examples, from weir studies) and then used to specify a Bayesian prior distribution (see Carlin and Louis 2000) for maximum-likelihood abundance and precision estimation. Su et al. (2001) modified the model of Hillborn et al. (1999) to account for declining longevity over the spawning season (e.g., Neilson and Geen 1981; English et al. 1992; Korman et al. 2002) and also developed a hierarchical Bayesian method to use historical information on peak abundance and longevity to reduce uncertainty of estimates from incomplete time-series counts (Adkison and Su 2001). These customizations, while clearly more flexible than the traditional AUC approach, all retain a strong dependence on the prior estimate for longevity. Consequently, large errors in the abundance estimate can arise when the true longevity departs sufficiently from the assumed prior. In addition, because of the restrictions imposed on the parametrical model, there appears to be no way to infer mortality dynamics directly from the abundance counts.

In this paper, we develop a method for estimating both mortality and abundance from a single time series of live-spawner counts, eliminating the need for prior or auxiliary information on longevity. Our approach is model-dependent, requiring the assumptions that all salmon die after spawning (i.e., they are semelparous; cf. Korman et al. 2002) and that the expected abundance change in the stream can be described as an arrival–death process. Our method closely follows that of Manly (1974) and Zonneveld (1991) for estimating mortality and abundance of emergent insects from serial transect counts, but departs where we allow mortality rates to change over time (see also Su et al. (2001)). Like both traditional AUC and the newer likelihood models (Hilborn et al. 1999; Su et al. 2001), our method requires additional information about detection rates in order to estimate abundance. However, we develop a model approximation that permits estimation of mortality even for cases when detection rates are unknown.

We present our approach in several steps. First, we introduce our model for the expected arrival and death dynamics. For simplicity, we begin by assuming that the rate of mortality is constant and then relax this assumption to allow for mortality rates that change linearly with time. Next, we develop a likelihood model that admits errors due to counting and uncertainty in the visual detection of fish for estimating mortality and abundance when estimates of detection rate are available for every count in the time series. Then we develop a second form of the likelihood to accommodate some missing estimates of detection. In addition, because data on detection may be available only as single-point estimates or, more often, lacking altogether from spawner surveys, we present an approximate likelihood model to estimate mortality and abundance using a single value for detection rate or to estimate only mortality when detection rates are entirely unknown. We use simulations to assess bias in estimates from this approximation under different parameter values. Finally, we demonstrate the methods using data that were collected in a tag-and-survey study for adult coho salmon (*Oncorhynchus kisutch*) in northern California where abundance was known from a weir.

Methods

Modeling arrival and death

For semelparous species such as coho salmon, the number of live fish that are present in a stream at time t ($x(t)$), and therefore susceptible to visual sampling, depends largely on two biological processes: (*i*) arrival to the stream or the sample area and (*ii*) mortality or permanent emigration (Quinn and Gates 1997). Where sampling covers the entire stream length, removals from the sample are due mostly to mortality, and in this case, the inverse of the mortality rate (days^{-1}) is equivalent to the adult longevity (sometimes called "stream-residence time" (English et al. 1992) or "stream life" (Hilborn et al. 1999)). When only part of the stream is sampled, the longevity estimate will include both mortality and permanent emigration.

To model the counting process through time, we first define the rate of abundance change, $\mathrm{d}x(t)/\mathrm{d}t$, as the instantaneous difference between the number of new arrivals and new deaths (Manly 1974; Zonneveld 1991; Quinn and Gates 1997). For simplicity, we assume that the overall pattern of arrival can be modeled by a two-parameter gamma density curve having

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mode at time $t = (r - 1)/\lambda$, where $r \geq 1$ and $\lambda > 0$. The advantage of modeling arrival by a parametric curve is that the density function is assured to integrate to unity, thus permitting the total escapement to be modeled despite intermittent observation (Hilborn et al. 1999; Su et al. 2001; Korman et al. 2002). We selected the gamma curve because the gamma density function is constrained to the positive numbers and because it can take a wide variety of shapes, including asymmetrical ones. Below we model mortality as constant or changing linearly with time. The expected rate of abundance change is then given by the proportion of total escapement arrived at time t minus the expected deaths at time t.

Constant mortality

With constant per-capita mortality (θ), the rate of abundance change is given by

$$(1) \qquad \frac{dx(t)}{dt} = E\frac{\lambda^r t^{r-1} e^{-\lambda t}}{\Gamma(r)} - \theta x(t), \quad t \geq 0$$

where E is the total escapement, $\Gamma(r)$ is the normalizing gamma constant

$$\Gamma(r) = \int_0^\infty y^{r-1} e^{-y} dy$$

and λ and r are positive constants to be estimated from the time-series counts. The solution to eq. 1 for E is

$$E = \theta \int_0^\infty x(t) dt$$

which is the total number of fish that died and is equivalent to the AUC solution for the total escapement. By noting that eq. 1 is a first-order linear differential equation, it can be analytically solved for $x(t)$ (see, e.g., Boyce and DiPrima 2004). The solution for $x(t)$, with initial condition $x(0) = 0$, yields the expected number-present curve:

$$(2) \qquad x(t) = E\alpha \int_0^t \frac{\lambda - \theta)^r u^{r-1} e^{-u}}{\Gamma(r)} du, \quad t \geq 0$$

where $\alpha = [\lambda/(\lambda - \theta)]^r e^{-\theta t}$ for $\lambda > \theta$. Under this model, abundance rises to a peak at $t = (r - 1)/(\lambda - \theta)$, then declines smoothly toward zero as t becomes large. For any time t, the expected number of live fish present and susceptible to sampling depends on four parameters: the total escapement (E), the mortality rate (θ), and the two arrival parameters of the gamma density function (r and λ).

Nonconstant mortality

To accommodate potentially increasing (or decreasing) mortality with time, we assume linear change and substitute θ in eq. 1 with $\theta(t) = \theta_0 + \theta_1 t$, where $\theta_0 > 0$ is the initial mortality rate and θ_1 is the coefficient of mortality acceleration. The linear model, while potentially restrictive for the overall pattern of mortality, may be considered a first-order approximation to a more complicated rate function (e.g., Quinn and Gates 1997; Su et al. 2001) that otherwise might be too difficult to estimate precisely from a short time series of counts. The solution for $x(t)$, with $x(0) = 0$, yields

$$(3) \qquad x(t) = Ee^{-b} \int_0^t \frac{\lambda^r u^{r-1} e^{c-\lambda u}}{\Gamma(r)} du, \quad t \geq 0$$

where

$$b = \int_0^t \theta(v) dv = \theta_0 t + 0.5\theta_1 t^2$$

and

$$c = \int_0^u \theta(v) dv = \theta_0 u + 0.5\theta_1 u^2, \quad u \geq 0$$

Note that for $\theta_1 = 0$, the mortality rate is constant and that this solution returns eq. 2 as a special case. Model selection for mortality dynamics may therefore proceed in the form of a statistical test on the value of the acceleration coefficient.

Admitting unpredictable variability

Random variation can be introduced to the model in one of three ways: (*i*) as process variability in arrival and death dynamics (Quinn and Gates 1997); (*ii*) as sampling variability due to counting errors and differences in detection rates during multiple visual surveys (Quinn and Gates 1997; Hilborn et al. 1999; Su et al. 2001); or (*iii*) as both process and sampling variability (Parken et al. 2003). Immigration and death are likely to vary as a consequence of biology and environmental conditions. However, this variation often is difficult to infer with intermittent observations because most irregular features of immigration and death are effectively removed (or smoothed) from the data as a result of counting fish that arrived or died over multiple surveys. For simplicity, we shall assume that process variability has a negligible effect on the data and that most of the observable variation in our counts arises from sampling.

A likelihood model

Our inferential model therefore takes the form of a sampling model for a series of observations from the realized number-present curve. During each of q survey occasions, the entire stream is sampled and n_u ($u = t_0, t_1, \ldots, t_{q-1}$) individual fish are counted. We assume that each individual that is alive and present in the stream on occasion u is detected with frequency π_u, where the detection frequencies themselves are independently and identically distributed (iid) as beta random variables. The beta density function for detection is

$$(4) \qquad f(\pi_u) = \frac{\Gamma(\alpha+\beta)}{\Gamma(\alpha)\Gamma(\beta)} \pi_u^{\alpha-1}(1-\pi_u)^{\beta-1},$$

$$0 \leq \pi_u \leq 1 \text{ and } \alpha, \beta > 0$$

with mean $E(\pi_u) = \alpha/(\alpha + \beta)$. Thus, the unconditional distribution of a count from the number-present curve ($x_u = x(u)$) is

$$(5) \qquad g(n_u) = \int_0^1 p(N_u = n_u | \pi_u) f(\pi_u) d\pi_u$$

$$= \binom{x_u}{n_u} \frac{\Gamma(\alpha+\beta)}{\Gamma(\alpha)\Gamma(\beta)} \frac{\Gamma(\alpha+n_u)\Gamma(\beta+x_u-n_u)}{\Gamma(\alpha+\beta+x_u)}$$

with mean $x_u\alpha/(\alpha + \beta)$. Equation 5 can be recognized as a beta-binomial distribution (Carlin and Louis 2000), because

$$p(N_u = n_u | \pi_u) = \binom{x_u}{n_u} \pi_u^{n_u} (1-\pi_u)^{x_u - n_u}$$

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is a conditional (on π_u) binomial distribution. The important assumptions to this point are that the distribution of detection frequencies is homogeneous with respect to the individual fish and that the distribution of counts follows a conditional binomial distribution.

The necessary data for statistical inference include the time-series counts $n_{t_0}, n_{t_1}, \ldots, n_{t_{q-1}}$, and the time series of detection frequencies, which we shall treat separately below as being either fully or partially known. From the data, we wish to estimate the $x_1, x_2, \ldots$, or more precisely, by substituting eq. 2 or eq. 3 into to eq. 5, we wish to estimate the model parameters $[E, r, \lambda, \theta]$ in the case of constant mortality (eq. 2) or $[E, r, \lambda, \theta_0, \theta_1]$ in the case of nonconstant mortality (eq. 3).

If the full time series of detection frequencies is known (i.e., $\{\pi_{t_0} = p_{t_0}\}, \{\pi_{t_1} = p_{t_1}\}, \ldots, \{\pi_{t_{q-1}} = p_{t_{q-1}}\}$), the model likelihood L_1 is most easily expressed for parameter estimation as a binomial model for x_u:

$$(6) \qquad L_1 = \left[\prod_{u=0}^{q-1}\binom{x_u}{n_u} p_u^{n_u}(1-p_u)^{x_u-n_u}\right]$$

where u ($u = 0, 1, \ldots, q-1$) denotes survey occasions. Estimation of the unknown parameters then should proceed by replacing x_u with eq. 2 or eq. 3, with the necessary constraint that the detection rate on the first survey be some value greater than zero, and numerically maximizing the binomial component of the likelihood directly at the time-series counts.

We may accommodate some missing values for detection by assuming that the distribution of detection frequencies is identically distributed with respect to the separate survey occasions. Mean detection undoubtedly will vary over time in response to variable stream conditions, but the assumption of a stationary distribution for detection seems reasonable if sampling is scheduled to coincide with consistently favorable counting conditions, such as during low stream flow and during peak daylight. Under these assumptions the model likelihood then can be written

$$(7) \qquad L_2 = \left[\prod_{u=0}^{q-1}\binom{x_u}{n_u} p^{n_u}(1-p)^{x_u-n_u}\right] \times \left[\prod_{u=0}^{q-1}\frac{\Gamma(\alpha+\beta)}{\Gamma(\alpha)\Gamma(\beta)} p_u^{\alpha-1}(1-p_u)^{\beta-1}\right]$$

The advantage of this formulation for the likelihood is that the overall mean detection now can be estimated by the average of any two or more individual estimates of detection rate. Also, extra uncertainty is included in the model in the form of beta variability because full detection frequencies are unknown and must be estimated by the mean detection rate over time.

An approximate likelihood

The model likelihood can be recast in its most simple, albeit restrictive, form to estimate abundance and mortality if only a single-point estimate of detection is available or to estimate only mortality if detection estimates are entirely lacking. By assuming that detection rates are constant (i.e., $p_u = p$ for all u), the binomial distribution tends, for large samples, to a Poisson distribution with mean and variance equal to $\mu_u = px_u$. This leads to an approximate likelihood (e.g., Zonneveld 1991):

$$(8) \qquad L_3 = \prod_{u=0}^{q-1}\frac{(px_u)^{n_u}e^{-px_u}}{n_u!} = \prod_{u=0}^{q-1}\frac{\mu_u^{n_u}e^{-\mu_u}}{n_u!}$$

It should be noted that the Poisson distribution restricts the variance, which may mean that the widths of the confidence intervals (CIs) are somewhat underestimated (i.e., too narrow).

When detection rates are entirely unknown, abundance cannot be estimated by ML because p and E are completely confounded in the estimating equations. (This limitation is common to other ML methods as well, e.g., Hilborn et al. (1999) or Su et al. (2001).) However, the solutions to the ML equations $\partial L_3/\partial\theta = 0$ or $\partial L_3/(\partial\theta_0, \partial\theta_1) = (0,0)$ are not affected by the confounded parameters p and E, so an approximate ML estimate for mortality can be obtained despite having no information on the true level of escapement or the detection rate.

A simulation study to examine bias of the approximate likelihood

We performed Monte Carlo simulations to examine bias of mortality and abundance estimation under our approximate likelihood model. Using eqs. 3 and 7, we simulated 200 time series of eight counts (the number from our tag-and-survey study; see Demonstration of the approach) under each of 60 parameter combinations for mean detection, total escapement, and mortality acceleration θ_1. We assumed that beta variability in detection under eq. 3 incorporated observation error into the simulated data. To apply the results to small populations, we restricted the range of total escapement for simulations to between 350 and 1400. Values of the remaining parameters were selected based on our analysis of data from the tag-and-survey study and are presented with the results in Figs. 1 and 2. To each simulated time series, we fitted eq. 3 by iterative maximization of the natural logarithm of the Poisson likelihood (eq. 8), thus obtaining a total of 200 × 60 individual estimates for $[E, r, \lambda, \theta_0, \theta_1]$. From each set of 200, we estimated the median mortality-rate estimate, $M[\hat{\theta}(t)]$ and the asymptotic relative bias of the escapement estimate, $\mathrm{ARB} = (M[\hat{E}] - E)/E$.

Demonstration of the approach

Collection of empirical data

We collected empirical data on spawning coho salmon in the South Fork Noyo River, a small coastal river in northern California, to evaluate the performance of the models against empirical estimates of mortality and escapement. We conducted traditional spawner surveys to obtain counts of live adults for fitting the models and used counts of adult coho at a weir and mark–recapture surveys to estimate total escapement, longevity, and detection rates for comparison. We checked the weir daily during the entire coho spawning season, December 2003 to February 2004. Coho were measured, identified to sex, marked with an operculum punch and a uniquely numbered Floy tag (T-bar anchor tags; Floy Tag, Seattle, Wash.), and released upstream. We marked three groups of fish (100–240 each) with different-colored

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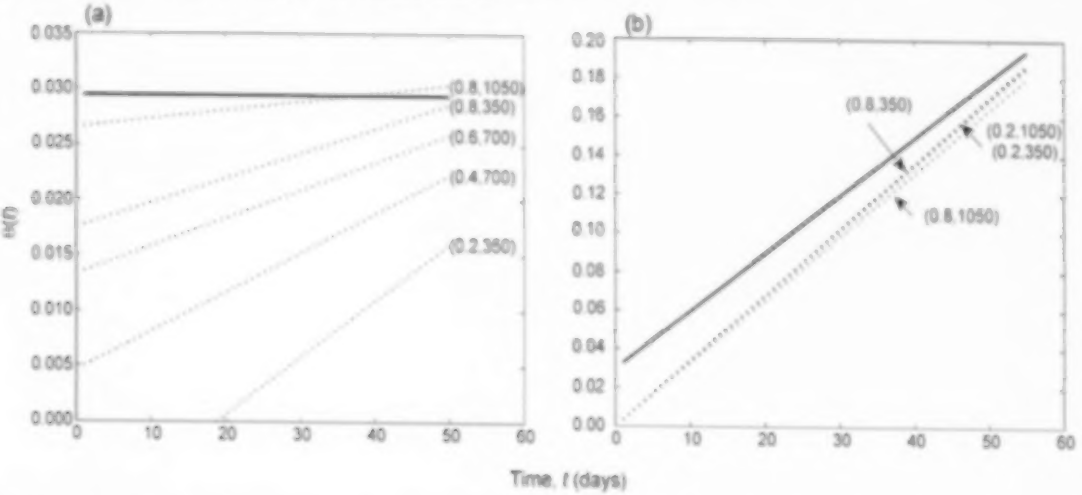
Fig. 1. Median mortality-rate estimates, $M[\hat{\theta}(t)]$, from simulated time-series counts as a function of mean detection and total escapement (π,E). The solid line in each plot indicates the basis mortality rate for simulations: $\theta_0 + \theta_1(t)$, with $\theta_0 = 1/34 = 0.029$ and (*a*) $\theta_1 = 0$ or (*b*) $\theta_1 = 0.003$. For clarity, some results are not shown.



tags on separate dates 1–2 weeks apart in December to estimate detection rates during subsequent spawner surveys. We counted live spawners and recovered tagged carcasses during approximately weekly surveys covering the entire habitat upstream of the weir, roughly 35 km of stream. We conducted surveys when stream flow and visibility were favorable until no new spawners or carcasses were found, for a total of eight surveys. For estimating longevity, we took the date of death as the midpoint between the survey when a carcass was found and the prior survey (to reduce overestimating stream life because of the intervals between surveys) and calculated longevity as the number of days between tagging of a fish at the weir and date of death. We estimated detection rate for each color-tagged group of fish as the proportion of tagged fish that was observed during the survey on the week after the group was tagged. We estimated escapement by adjusting the weir count using a Petersen estimate to account for unmarked carcasses that were found above the weir. To resolve variation in the longevity data, we fitted a multiple-regression model with longevity taken as the dependent variable and sex, fork length, arrival day, and sex-by-day interaction taken as independent variables.

Model fitting and testing

We fitted models for constant and nonconstant mortality to the time-series counts from spawner surveys using, for demonstration, both L_2 (beta-binomial likelihood) and L_3 (Poisson likelihood) to compare parameter estimates under the different likelihooods. Each model was fitted by iteratively maximizing the natural logarithm of the particular likelihood using the simplex search algorithm (Lagarias et al. 1998) in MATLAB (The MathWorks Inc. 2004). Integrals for calculating abundance were evaluated numerically at each iteration of the search procedure by adaptive Gauss–Lobatto quadrature (Gander and Gautschi 2000). For detection rate, we used 0.22 (mean from the tagging estimates) and also 0.50 and 0.70 for comparison because the empirical values probably underestimated actual detection (see Results below). We made pairwise comparisons between mortality models (constant vs. nonconstant) using G^2 tests (generalized likelihood-ratio tests; Rice 1995) to compare quality of fits to the data.

Precision, bias, and correlations of the parameter estimates were estimated by parametric bootstrap (Bradley and Tibshirani 1993). For the data, we simulated 2000 time series of eight counts under eqs. 3 and 7, with parameters substituted by their ML estimates and selecting a detection rate that yielded an escapement estimate closest to the weir count for ease of comparison. Sampling distributions were generated by refitting the model to each simulated time series. Precision was estimated by the percentiles of the empirical sampling distribution and by the coefficient of variation (CV) = SD/median. In this case, CIs may be underestimated somewhat because of our choice of a fixed detection rate and our use of a Poisson model that does not accommodate overdispersion. Bias was estimated by ARB = (median – estimate)/estimate.

Results

Simulations using the approximate likelihood

Median mortality-rate estimates from the Monte Carlo simulations for constant mortality ($\theta_1 = 0$) showed an inverse relationship between estimates of θ_0 and θ_1, indicating negative bias in $\hat{\theta}_0$ with positive bias in $\hat{\theta}_1$ (Fig. 1*a*). As a consequence of this relationship, estimates of mortality acceleration, which should equal zero, were instead positive, implying an increasing rate of mortality through time and resulting in a change from negative bias in the mortality estimate at $t = 0$ to eventually positive bias. The degree of bias appeared to diminish over the higher levels of detection and total escapement, and for $\pi \approx 0.80$ and $E \geq 1050$, the mortality estimate did not differ much from its basis value of $\theta_0 = 0.029$ (determined from the tag-and-survey study).

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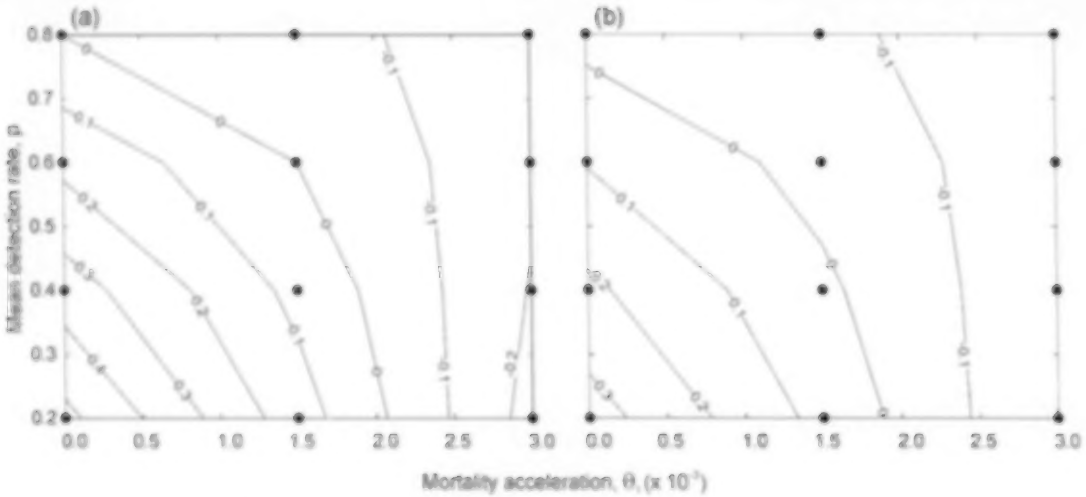
Fig. 2. Asymptotic relative bias (ARB) for estimates of total escapement from simulated time-series counts as a function of parameters π and θ_1. Each solid circle represents 200 estimates from data simulated under a binomial probability distribution with values $r = 2.68$, $\lambda = 0.16$, and $\theta_0 = 0.029$ and (*a*) $E = 350$ or (*b*) $E = 1400$. Contours were fitted using a linear-interpolation algorithm in MATLAB (The MathWorks 2004).



For nonconstant mortality ($\theta_1 > 0$), estimates of θ_0 and θ_1 also were inversely related, but in contrast to the previous case, the degree of bias generally was insensitive to variability in mean detection and escapement (Fig. 1*b*). Although we set $\theta_0 = 0.029$ for all simulations, estimates of θ_0 never deviated much from zero, suggesting, at least for these data, that the initial mortality was difficult to estimate. Estimates of θ_1 were higher than the basis value in all cases.

Despite the bias observed in the mortality-rate estimates (Fig. 1), escapement estimation appeared to be little affected by Poisson approximation (Fig. 2). This is because the total escapement can be considered a weighted sum of the mortality and the number present, $E = \int_0^\infty \theta(t)x(t)dt$, and therefore bias in the escapement estimates is incurred largely as a function of the estimated net mortality, $\int_0^\infty \hat{\theta}(t)dt$, rather than the estimated instantaneous mortality, $\hat{\theta}(t)$. For instance, where bias in the estimates of instantaneous mortality was negative and then positive and large (over low θ_1 and low π; Fig. 2*a*), the net mortality was overestimated, and as a result, the escapement was estimated high (lower diagonals of Figs. 2*a*, 2*b*). Conversely, where bias in the estimates of instantaneous mortality were negative and small (over high θ_1; Fig. 2*b*), net mortality was underestimated, and as a result, escapement was estimated low (upper diagonals of Fig. 2). Also, because the bias was little affected by detection and escapement for $\theta_1 > 0$ (Fig. 2*b*), the bias in the escapement estimates was generally unchanged over the basis values of π and E. For $\theta_1 > 0$, the amount of bias often was small (mostly between –20% and 20%; Fig. 2*b*).

Demonstration of the approach

Empirical results

We captured and marked 645 adult coho at the South Fork Noyo River weir (Fig. 3) and recovered 162 carcasses during spawner surveys. Fourteen of the carcasses were unmarked, resulting in a Peterson estimate of total escapement of 706 fish. Estimates of detection rate from the three groups of uniquely tagged fish were 0.24, 0.20, and 0.22, suggesting that detection frequencies were stationary over time and that eq. 7 was an appropriate likelihood for parameter estimation. However, the mean detection rate ($\hat{p} = 0.22$) probably underestimated true detection as a result of unobserved mortality and tag loss (e.g., 35% of carcasses had operculum punches but were missing Floy tags). Multiple regression analysis revealed that longevity was related to arrival day (type III F tests, with $\alpha = 0.05$, $b = -0.51$, $F = 31.09$, $P < 0.001$, $R^2 = 0.25$, $n = 92$) but unrelated to sex or size, with no interactions. The final fitted regression for the mean longevity shows a steep decline from approximately 30 days at the start of the immigration period to approximately 10 days on the 40th day of the season (Fig. 4).

Performance and comparison of models

Estimates of per-capita mortality and total escapement, as well as the negative of the maximized log-likelihood ($-\ln L_{max}$) for model selection and evaluation of model goodness-of-fit, are shown in Table 1. The model for nonconstant mortality ($\theta_1 \neq 0$) provided a significantly better fit to the counts than the model for constant mortality, regardless of the level of detection or whether the test statistic was taken as a ratio of beta-binomial or Poisson likelihoods (Table 1). However, comparison of fits between the model for nonconstant mortality and a general model, in which the x_t were taken directly as the counts themselves rather than being estimated by eq. 3, yielded G^2 values of 30.0 for the Poisson and 28.1, 42.3, and 67.9 for the beta-binomial with $p = 0.22$, 0.5, and 0.7, respectively. Considering that the critical value for the test is $G^2_{\alpha,\nu} = 6.25$ (from a chi-square distribution with $\alpha = 0.1$ and $\nu = 3$ df), the large values indicated a significant model lack-of-fit (when compared with the most general model) and that the data were better described with more pa-

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Fig. 3. Daily counts of coho salmon at the South Fork Noyo River weir. Day 0 marks the time of the first upstream spawner survey.

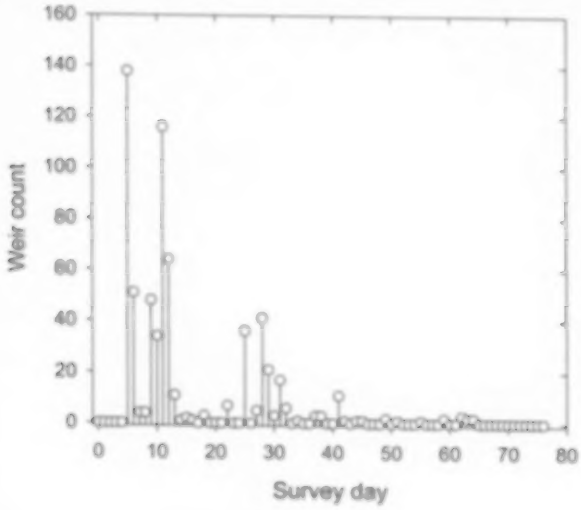
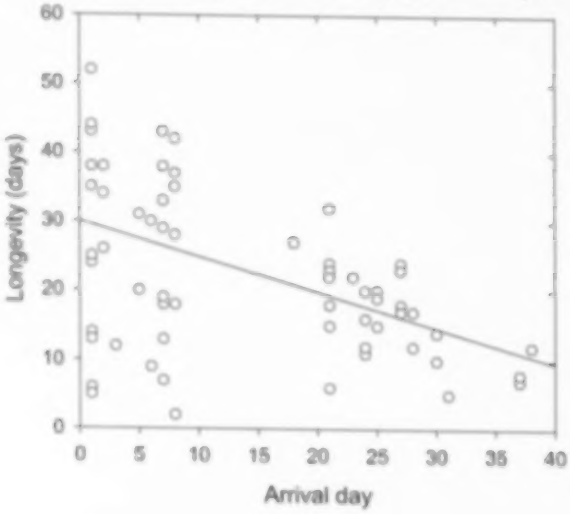


Fig. 4. Longevity of adult coho salmon with respect to arrival day at the South Fork Noyo River weir (linear regression, $y = 30.03 - 0.51x$, $P < 0.001$, $R^2 = 0.25$). Longevity was estimated from the recovery of tagged carcasses during spawner surveys.



rameters. Nonetheless, the nonconstant mortality model shows a reasonably good fit to the counts (Fig. 5), which is heartening in light of the irregular pattern of arrival that we observed at the weir (Fig. 3).

Most differences between the escapement estimates were due to differences in average detection and whether mortality was taken as constant or nonconstant rather than due to differences in the assumed likelihood distribution (Table 1). Estimates of escapement between likelihoods were virtually identical for models of constant mortality but were lower under the Poisson distribution, because of negative bias in estimates of net mortality (see Simulations using the approximate likelihood) for models of nonconstant mortality. The escapement estimate closest to the weir count was obtained by the nonconstant mortality model with $p = 0.50$, suggesting, if the model is correct, that our three mark-resighting surveys underestimated mean detection of tagged fish (as noted above) and that the average detection may indeed have been closer to 0.50. Escapement estimates by the constant mortality model were always about twice that estimated by the nonconstant mortality model and were always much higher (by a factor of 1.67–5.33) than the weir count.

Initial parameter estimates and the bootstrap results for estimating precision, bias, and correlations of the parameter estimates are shown in Table 2. On eight counts, estimates were generally accurate but imprecise, with ARB $\leq$ |0.05| and CV ≤ 0.5. Estimates of intrinsic mortality (θ_0) were highly imprecise, but the estimates were close enough to zero to have little practical importance. Note that the bootstrapped 90% CI for $\hat{\theta}_1$ does not include zero, suggesting that our decision to include θ_1 in the model was correct. The 50th percentile of our model-based longevity estimate (the inverse of the mortality-rate estimate) was 7.3 days (90% CI: 4.1,10.1) at $t = 40$, which is similar to the empirical estimate based on tagging (Fig. 4). Correlations between $\hat{r}$ and $\hat{\lambda}$ and between $\hat{\lambda}$ and $\hat{\theta}_1$ were high, indicating that several combinations of parameter values could describe the arrival and mortality pattern in the data equally well. The high correlation between $\hat{E}$ and $\hat{\theta}_1$ reflect the strong dependence of the escapement estimate on the estimate of mortality rate.

Discussion

The AUC approach for abundance estimation lends naturally to statistical modeling because the escapement process can be partitioned straightforwardly into manageable components of arrival and death. Likelihood methods admit uncertainty in the underlying components because of process or sampling variability, as well as provide a general framework for statistical inference. In this paper, we relied on the setting of differential equations, put forth by Quinn and Gates (1997), to model the escapement process through time. Autocorrelation in arrival was managed by modeling immigration by parametric density function (Hilborn et al. 1999), and mortality was modeled, on a per-capita basis, as constant (Manly 1974; Zonneveld 1991) or changing linearly over time. The solution to the differential equation yielded our model for the expected number present, which we incorporated as the mean of a beta-binomial or Poisson probability model to allow for variability from sampling. Conditional on the model, we extracted information on deaths from the time-series counts by explicitly accounting for the effect of mortality on the location of the peak and on the rate of change in the fitted number-present curve. Our results from applying the model to count data on coho salmon from South Fork Noyo River gave accurate estimates of mortality compared with empirical estimates based on tagging and produced reasonable estimates of abundance within the uncertainty surrounding the detection rate.

The major improvement of our approach over previous AUC and likelihood methods is the ability to estimate mortality directly from time-series counts of spawners, eliminating the need to collect additional data on mortality rates.

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Table 1. Estimates of parameters for models of constant mortality θ and nonconstant mortality $\theta(t)$ fit to counts of adult coho from the South Fork Noyo River in 2003–2004.

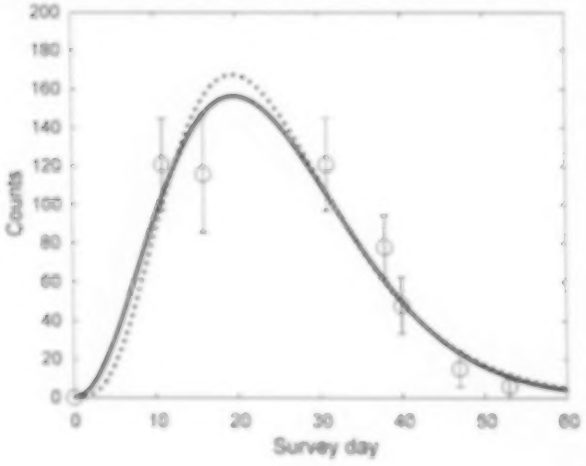
Model	p	$-\ln L_{max}$	$\hat{E}$	$\hat{\theta}_0$	$\hat{\theta}_1$	G^2	P value[a]
Beta-binomial							
θ	0.22	38.19	3764	0.189			
θ	0.50	46.59	1655	0.186			
θ	0.70	61.82	1182	0.182			
$\theta(t)$	0.22	32.94	1710	1.73×10^{-6}	3.52×10^{-3}	10.50	1.20×10^{-3}
$\theta(t)$	0.50	38.72	727	1.84×10^{-9}	3.37×10^{-3}	15.73	7.31×10^{-5}
$\theta(t)$	0.70	49.76	522	—[b]	3.32×10^{-3}	24.10	9.13×10^{-7}
Poisson							
θ	0.22	34.98	3765	0.191			
θ	0.50	34.98	1656	0.191			
θ	0.70	34.98	1183	0.191			
$\theta(t)$	0.22	30.81	1593	—[b]	3.31×10^{-3}	8.35	3.86×10^{-3}
$\theta(t)$	0.50	30.81	701	—[b]	3.31×10^{-3}	8.35	3.86×10^{-3}
$\theta(t)$	0.70	30.81	501	—[b]	3.31×10^{-3}	8.35	3.86×10^{-3}

Note: Parameters were estimated using a beta-binomial or Poisson likelihood and under different levels of mean detection p. Escapement (E), estimated at the weir, was 706.

[a]Probability value for $G^2 = 2\ln L_{max,A} - 2\ln L_{max,B}$, from a chi-square distribution with $v = 1$ df.

[b]$\hat{\theta}_0 < 1 \times 10^{-9}$.

Fig. 5. Estimates of coho salmon abundance (lines; scaled by detection rate $\hat{p} = 0.22$) and the number of live fish counted during periodic walking surveys of the South Fork Noyo River (circles). Error bars for counts are ±2 SE, estimated from a beta-binomial distribution. Day 0 marks the time of the first survey. The model-based abundance estimates account for either a constant (dotted line) or increasing (solid line) rate of in-stream mortality.



This should reduce the time and cost where tagging (e.g., English et al. 1992) or other techniques (e.g., video; Shardlow 2004) otherwise would be used to estimate mortality and should improve the accuracy of estimates when estimating mortality is not practical and average values from the literature would be used instead. Furthermore, our method allows modeling of decreasing longevity over the spawning season, which improves the accuracy of escapement estimates compared with using constant values (our study; Su et al. 2001). The nonconstant mortality (i.e., decreasing longevity) model better fit the data than the constant mortality model under both likelihoods (beta-binomial and Poisson) and provided an abundance estimate much lower and closer to the weir count, and thus the form of the mortality model had a much greater effect on the abundance estimate than the form of the likelihood. The mortality estimates also were largely insensitive to the detection rate, especially under the nonconstant model.

In our paper, we worked from general forms of the models to simpler forms by imposing constraints based on logical assumptions, and the various forms of the models allow flexibility in applying the method under different data scenarios. As mentioned earlier, the nonconstant mortality model generally appears to be more suitable than the constant mortality form, although selection of the mortality form can be tested for individual data sets. The different forms of the likelihood cater to different levels of information on detection rate. If detection rates are estimated for every count in the time series (such as by using distance sampling; see below), L_1 (eq. 6) can be used. L_2 (eq. 7) is useful if some detection estimates are missing from the time series but enough data is available to calculate the mean or if enough prior information is available (or alternatively might be taken from the literature) to specify parameters for the beta distribution for detection. The approximate likelihood L_3 (eq. 8) is useful for estimating abundance and mortality if only a single-point estimate of detection is available or for estimating just mortality in the absence of any detection rate information. The Monte Carlo simulations and the similarity of results between fitting the counts in the demonstration using the beta-binomial versus the Poisson likelihood suggest that the approximate (Poisson) likelihood offers a relatively unbiased and simple model that may be used in these cases.

Although our model offers several refinements over past methods, it shares two limitations common to all AUC approaches. First, our model requires the initial-condition constraint, $x(0) = 0$. This constraint was necessary to obtain the

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Table 2. Initial parameter estimates and bootstrap results from simulations of the South Fork Noyo River coho counts using the nonconstant mortality model (eqs. 3 and 7), with $p = 0.5$.

(*a*) Initial parameter estimates.

		Percentile				
Parameter	Estimate	5	50	95	CV	ARB
E	727.3	533.8	741.6	1379.7	0.488	0.020
r	2.588	2.122	2.708	4.099	0.252	0.047
λ	0.149	0.105	0.148	0.291	0.444	–0.010
θ_0	1.84×10^{-9}	—[a]	—[a]	—[a]	1.077	–0.050
θ_1	3.37×10^{-3}	2.48×10^{-3}	3.42×10^{-3}	6.14×10^{-3}	0.465	0.014

(*b*) Correlation coefficients.

	$\hat{E}$	$\hat{r}$	$\hat{\lambda}$	$\hat{\theta}_0$
$\hat{r}$	–0.04			
$\hat{\lambda}$	–0.39	0.91		
$\hat{\theta}_0$	0.03	0.03	0.04	
$\hat{\theta}_1$	0.99	–0.06	–0.40	0.03

Note: A time-series of eight counts was simulated 2000 times. ARB, asymptotic relative bias.
[a] $\theta_0 < 1 \times 10^{-8}$.

solution (eq. 2 or eq. 3) for the expected rate of abundance change (eq. 1) and follows because the gamma density at $t = 0$ is equal to zero. The analogous constraint in AUC estimation is that the first and last counts must equal zero (English et al. 1992), but with the parametric approach only the first count must be so constrained. If fish are present on the first survey, the day of first arrival to the sample area must be guessed or estimated and the time series incremented accordingly. Otherwise, the first count in the series will be disregarded in estimation (i.e., assumed to be zero), thus leading to an error in the mortality and escapement estimates. The use of historical data may help to specify a Bayesian prior distribution on arrival time in the spirit of Su et al. (2001), but the easiest solution is to schedule surveys to occur either before or soon after the start of arrival. Unfortunately, such precise scheduling may not always be realistic.

The second limitation is the requirement for information on detection rate to estimate escapement. Because visibility rates for surveys often are poorly resolved, estimates of salmon abundance may be particularly susceptible to this form of uncertainty. The standard method of detection estimation is to take a two-stage sampling approach and "correct" visual counts by correlation with a set of independent abundance estimates obtained using more rigorous methods of enumeration (e.g., photography (Neilson and Geen 1981); electrofishing or snorkeling (Irvine et al. 1992); walking versus arial counts (Hilborn et al. 1999); mark and recapture (Lady and Skalski 1998; Manske and Schwarz 2000; Korman et al. 2002)). We took a similar approach, using a series of tag and resight surveys to collect data on detection. However, this approach was shown to be unreliable in practice because constraints on surveyor effort prevented more than three attempts at data collection, some level of tag loss occurred, and sampling conditions delayed the resighting surveys, resulting, presumably, in underestimates of the mean detection rate. Therefore, despite expending considerable effort and using a weir for tagging, we could generate only a small number of data to infer detection, which in addition to compromising accurate estimation of the mean also made it impossible for us to rigorously evaluate assumptions of detection homogeneity and stationarity.

In conclusion, although our method reduces one of the data limitations for estimating salmon spawner abundance from standard stream counts by estimating longevity directly from the counts, a robust method of determining detection still is sorely needed to improve the accuracy of escapement estimates. One method that deserves serious consideration is distance sampling, in particular, line-transect sampling (Buckland et al. 1993). Line-transect sampling has found wide use in visual surveys of marine mammals (Laake et al. 1997; Gelatt and Siniff 1999; Pollard et al. 2002) and reef fishes (Watson and Quinn 1997; Kulbicki 1998; Samoilys and Carlos 2000) but has not been used much in streams (however, see Ensign et al. 1995). The theoretical basis for the method is that the probability of detection within a surveyed area declines from unity as a predictable function of distance between the object of interest and the observer. A large statistical literature exists for inferring detection functions from counts, data on distances, and any potentially important covariates (e.g., stream clarity, depth, habitat variables). We believe that by incorporating such methods, for which our models are easily modified, the model-based approaches would be largely improved, thus yielding a more mature methodology of count-based escapement estimation.

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References

Adkison, M.D., and Su, Z.M. 2001. A comparison of salmon escapement estimates using a hierarchical bayesian approach versus separate maximum likelihood estimation of each year's return. Can. J. Fish. Aquat. Sci. **58**: 1663–1671.

Boyce, W.E.E., and DiPrima, R.C. 2004. Elementary differential equations. 8th ed. John Wiley & Sons, New York.

Bradley, E., and Tibshirani, R. 1993. An introduction to the bootstrap. Monographs on statistics and applied probability 57. Chapman & Hall, New York.

Buckland, S.T., Anderson, D.R., Burnham, K.P., and Laake, J. 1993. Distance sampling: estimating abundance of biological populations. 1st ed. Chapman & Hall, London, UK.

Carlin, B.P., and Louis, T.A. 2000. Bayes and empirical Bayes methods for data analysis. 2nd ed. Chapman & Hall, New York.

English, K.K., Bocking, R.C., and Irvine, J.R. 1992. A robust procedure for estimating salmon escapement based on the area-under-the-curve method. Can. J. Fish. Aquat. Sci. **49**: 1982–1989.

Ensign, W.E., Angermeir, P.L., and Dolloff, C.A. 1995. Use of line transect methods to estimate abundance of benthic stream fishes. Can. J. Fish. Aquat. Sci. **52**: 213–222.

Gander, W., and Gautschi, W. 2000. Adaptive quadrature — revisited. BIT. **40**: 84–101.

Gelatt, T., and Sini, D. 1999. Line transect survey of crabeater seals in the Amundsen–Bellingshausen seas, 1994. Wildl. Soc. Bull. **27**: 330–336.

Hilborn, R., Bue, B.G., and Sharr, S. 1999. Estimating spawning escapements from periodic counts: a comparison of methods. Can. J. Fish. Aquat. Sci. **56**: 888–896.

Irvine, J.R., Bocking, R.C., English, K.K., and Labelle, M. 1992. Estimating coho salmon (*Oncorhynchus kisutch*) spawning escapements by conducting visual surveys in areas selected using stratified random and stratified index sampling designs. Can. J. Fish. Aquat. Sci. **49**: 1972–1981.

Korman, J., Ahrens, R.N.M., Higgins, P.S., and Walters, C.J. 2002. Effects of observer efficiency, arrival timing, and survey life on estimates of escapement for steelhead trout (*Oncorhynchus mykiss*) derived from repeat mark–recapture experiments. Can. J. Fish. Aquat. Sci. **59**: 1116–1131.

Kulbicki, M. 1998. How the acquired behaviour of commercial reef fishes may influence the results obtained from visual censuses. J. Exp. Mar. Biol. Ecol. **222**: 11–30.

Laake, J., Calambokidis, J., Osmek, S., and Rugh, D. 1997. Probability of detecting harbor porpoise from aerial surveys: estimating g(0). J. Wildl. Manag. **61**: 63–75.

Lady, J.M., and Skalski, J.R. 1998. Estimators of stream residence time of Pacific salmon (*Oncorhynchus* spp.) based on release–recapture data. Can. J. Fish. Aquat. Sci. **55**: 2580–2587.

Lagarias, J., Reeds, J.A., Wright, M.H., and Wright, P.E. 1998. Convergence properties of the Nelder–Mead simplex method in low dimensions. SIAM J. Optimization, **9**: 112–147.

Manly, B.F.J. 1974. Estimation of stage-specific survival rates and other parameters for insect populations developing through several stages. Oecologia, **15**: 277–285.

Manske, M., and Schwarz, C.J. 2000. Estimates of stream residence time and escapement based on capture–recapture data. Can. J. Fish. Aquat. Sci. **57**: 241–246.

Neilson, J.D., and Geen, G.H. 1981. Enumeration of spawning salmon from spawner residence time and aerial counts. Trans. Am. Fish. Soc. **110**: 554–556.

Parken, C.K., Bailey, R.E., and Irvine, J.R. 2003. Incorporating uncertainty into area-under-the-curve and peak count salmon escapement estimation. N. Am. J. Fish. Manag. 23: 78–90.

Pollard, J., Palka, D., and Buckland, S. 2002. Adaptive line transect sampling. Biometrics, **58**: 862–870.

Quinn, T.J., and Gates, R. 1997. Estimation of salmon escapement: models with entry, mortality and stochasticity. Nat. Resour. Model. **10**: 217–250.

Rice, J.A. 1995. Mathematical statistics and data analysis. 2nd ed. Wadsworth, Belmont, Calif.

Samoilys, M., and Carlos, G. 2000. Determining methods of underwater visual census for estimating the abundance of coral reef fishes. Environ. Biol. Fishes, **57**: 289–304.

Shardlow, T. 2004. Using time-lapsed video to estimate survey life for area-under-the-curve methods of escapement estimation. N. Am. J. Fish. Manag. **24**: 1413–1420.

Su, Z.M., Adkison, M.D., and Van Alen, B.W. 2001. A hierarchical bayesian model for estimating historical salmon escapement and escapement timing. Can. J. Fish. Aquat. Sci. **58**: 1648–1662.

The MathWorks Inc. 2004. MATLAB. The MathWorks, Inc., Natick, Massachusetts.

Watson, R., and Quinn, T. 1997. Performance of transect and point count underwater visual census methods. Ecol. Model. **104**: 103–112.

Zonneveld, C. 1991. Estimating death rates from transect counts. Ecol. Entomol. **16**: 115–121.

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Behavioral inferences from the statistical distribution of commercial catch: patterns of targeting in the landings of the Dutch beam trawler fleet

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Abstract: The objective identification of targeting behavior in multispecies fisheries is critical to the development and evaluation of management measures. Here, we illustrate how the statistical distribution of commercial catches can provide information on species preference that is consistent with economic data but not a simple function of price. Using the Dutch beam trawl fishery from 1998 to 2003, we show that the distribution of the $\log_{10}$-transformed catch rates of preferred species exhibit greater negative skews than less preferred species. Furthermore, subsets of the fleet employing spatially distinct strategies generate the expected patterns in the skews of their catch distributions. A simple model is presented to illustrate a behavioral mechanism for variation in skews and identify circumstances where it could apply. As a result of this analysis we propose that (*i*) catch distributions should be examined by species when investigating targeting behavior and (*ii*) changes in error structure over time can be expected in comparisons of catch statistics such as those used to create abundance indices or estimate fishing power.

Résumé : L'identification objective du comportement de ciblage dans les pêches multispécifiques est essentiel afin de mettre au point et d'évaluer les mesures de gestion. Nous illustrons ici comment la distribution statistique des captures commerciales peut fournir des renseignements sur les préférences des espèces qui sont en accord avec les données économiques, mais qui ne sont pas une fonction simple des prix. Prenant en exemple la pêche commerciale hollandaise au chalut à perche de 1998 à 2003, nous montrons que les distributions des taux de capture transformés en $\log_{10}$ des espèces préférées montrent des asymétries négatives plus importantes que celles des espèces moins désirables. De plus, des sous-ensembles de la flotte qui utilisent des stratégies particulières en fonction de l'espace produisent des distributions des captures avec les patrons d'asymétrie attendus. Nous présentons un modèle simple pour illustrer un mécanisme comportemental pour la variation des asymétries et pour identifier les conditions de son application. À la lumière de cette analyse, nous proposons (*i*) d'examiner les distributions des captures espèce par espèce lorsqu'on étudie le comportement de ciblage et (*ii*) de tenir compte des changements temporels de la structure d'erreur qu'on peut attendre dans les comparaisons des statistiques de capture, comme celles qu'on utilise pour définir des indices d'abondance ou pour estimer la puissance de la pêche.

[Traduit par la Rédaction]

Introduction

The definition of targeting, or directed effort, in multispecies fisheries is more easily stated than applied. Targeting is the direction of fishing activities toward the capture of one or more specific species. Identifying targeting patterns within commercial data is required to estimate fishing power (Stocker and Fournier 1984) and to perform accurate stock assessments (Biseau 1998). Perfect knowledge of targeting could be provided by fishers, but this detail is usually missing from commercial data sets. Instead, biologists performing stock assessments must infer targeting from the landings and effort records. Typically, targeting has been defined by the relative weight of the species in the catch (Ketchen 1964; Weisterheim and Foucher 1985; Salthaug and Godo 2001). Observed effort is assigned to species that occur above some threshold percentage: the "quantification level". The values of species are not always incorporated in the identification of directed effort even though they can influence fisher's decisions (Salas et al. 2004) and bias estimates of fishing power (Smit 1996).

More recently, multivariate methods have been used to define targeting topologically based on combined data on fishing location, gear, and species caught in a trip (Biseau and

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Gondeaux 1988; Ulrich and Andersen 2004). These analyses involve principle components analysis, cluster analysis, and related techniques. They can easily incorporate economic value, as well as landed weight (Lewy and Vinther 1994), though final classifications are often based on landed weight (Pelletier and Ferraris 2000).

Any quantitative analysis of fisheries data must consider their statistical distribution. Unfortunately, there are typically two issues in the application of linear methods such as analysis of variance (ANOVA) or regression to catch records. First, the data frequently contain a large number of zeros representing fishing activities that failed to catch the species being studied (Bannerot and Austin 1983). Second, the data are often highly skewed (Taylor 1953). Pennington (1983) suggested the analysis of catch data as a two-step process: the delta distribution. Initially, a binomial model is used to fit the probability of observing a non-zero catch. The non-zero values are then assumed to be lognormally distributed (the delta-lognormal distribution), though other distributions can be used (Aitchinson 1955). Generalized linear models (GLMs; McCullagh and Nelder 1989) provide a more flexible alternative for fitting the distribution of non-zero catches (Maunder and Punt 2004) and skewed catch rates (Mahévas et al. 2004). GLMs can also simultaneously treat zeros and non-zero values by employing Poisson errors and more flexibly using the Tweedie family of error distributions (Candy 2004). All of these approaches assume that the error structure is defined similarly among the areas, times, or vessel groups being compared.

Early fisheries work has often employed the logarithmic transformation to catch rate data prior to statistical analysis employing linear models (Kimura 1981), and this transformation was advocated even when the lognormal distribution did not strictly apply (Taylor 1953). When this transformation was successful, it implied that the underlying true distribution was reasonably approximated by a lognormal distribution.

In the 19th century, Galton recognized that a lognormal distribution would arise naturally from the statistical properties of multiplicative stochastic processes (Johnson and Kontz 1970). Its use increased throughout the 20th century. Applications to the study of natural phenomena employing analytical and graphical methods have been undertaken since the 1930s. In fisheries data, one possible generative process is provided by the cumulative effects of survival in sequential life stages (Hilborn and Mangel 1997). Successive random partitioning of available resources can also generate a lognormal distribution (Johnson and Kontz 1970). Today, the lognormal distribution remains topical in studies of ecological abundance (Halley and Inchausti 2002). However, distributions observed in fisheries data may be better represented by other distributions such as the gamma, Weibull, or negative binomial (Myers and Pepin 1990; Power and Moser 1999). These distributions may represent more complex stochastic processes, but more pragmatically, they are chosen to better reflect the pattern of observed variation. In this paper, we use the lognormal distribution as a parsimonious reference point with a historical basis in fisheries analysis, while acknowledging that natural fish abundances may more closely follow a different statistical distribution in their environment.

The survey data used in fisheries analysis usually come from randomized designs, but in contrast, commercial fishing is not random. Knowledge about fish distributions should allow fishers to focus their effort on more profitable locations and bias their catches towards larger values (Rijnsdorp et al. 2000*a*). This will result in distributions that are more skewed towards higher abundances than in the underlying natural distribution. Thus, a direct examination of skews in catch rate distributions may provide information on targeting to complement other methods of identifying target species. Furthermore, the nature of the relationship between targeting and skew could impact the validity of the assumptions underlying the analysis of the fisheries data spanning areas or times with different economic incentives.

Our goals in this paper are (*i*) to develop the theoretical relationship between targeting behavior and catch rate distributions, (*ii*) to introduce methods for examining this relationship in field data, and (*iii*) to use these methods to examine targeting behavior in the Dutch beam trawl fleet in the North Sea. We will examine patterns in both landed weights and economic data in comparison with targeting suggested by the distribution of commercial catch rates.

Materials and methods

The simulation model

The simulation model represents the interaction between the distribution of fish and fishing behavior that creates the distribution of observed catches resulting from a standard unit of effort. Here catches are synonymous with catch rates when effort is standardized by some unit of time such as a day of fishing. The environment is modeled by an array of sites containing fish that are known to the fishers. This array did not represent any particular spatial arrangement of sites. It was a one-dimensional vector the index of which was the site's identity (site 1, site 2,..., site 10 000).

In reality, fish will be distributed in a manner related to local bottom type, depth, and other factors. However, regardless of the complexity of the environment, if fishers know the location of the sites where fish are found, we can focus on their choice among the occupied sites and ignore unoccupied sites when examining the impact of their decisions. For both simplicity and generality, we do not consider explicit spatial arrangements of sites in this simulation. Such arrangements are vast in number and would require a more complex model involving explicit movement and travel costs. Furthermore, the impact of these arrangements would be situation-specific. Thus, our model is an illustration of a general phenomena based on fisher choice rather than a representation of any one fishery.

We represented the local abundance of fish (N_i) as lognormally distributed among i sites where fish occurred. This was implemented by raising 10 to the power of a normally distributed random variable x:

$$(1) \qquad N_i = 10^{x_i}$$

$$P(x;\mu,\sigma) = \frac{1}{\sigma\sqrt{2\pi}} e^{-(x-\mu)^2/2\sigma^2}$$

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where $\mu = 0.5$ and $\sigma = 0.25$. These numbers were chosen to roughly approximate tonnes of fish and to keep subsequent calculations within the numerical limits of the computer (a Pentium IV desktop). However, we did not choose parameters to represent any specific fishery but to illustrate the general principles being examined. We worked in base 10 rather than base e, using $\log_{10}$ rather than $\log_e$ for transformations, as this scale is commonly used in fisheries analysis. The utility of the log transformation in "normalizing" data or stabilizing variance is independent of the base employed (Quinn and Keough 2002) and thus our choice of base will have no bearing on our results. Equation 1 allocated fish to each site, creating sites with varying positive abundances of fish. All sites received some fish initially so the simulated fish abundances follow the non-zero catches of a delta-lognormal distribution (Pennington 1983).

The fishing rate experienced within a site was modeled as a simple exponential decline within each fishing site during the season. This follows the assumptions of classical fisheries analysis (Hilborn and Walters 1992). In our simulation, the effects of natural mortality were not considered. This is analogous to a fishery occurring over a brief time span and during a time of relatively low natural mortality. Each simulated catch was assumed to result from a single unit of effort representing all fishing activity by a vessel within a single site during one time period, analogous to a day, in the simulation. Thus, these daily catches were equivalent to catch per unit effort. As a baseline, a typical simulated season contained 2500 units of effort. In addition, seasons with intensive fishing were simulated by 10 000 units of effort. Each unit of effort was simulated sequentially until all of the seasonal effort was expended. There were no explicit spatial dynamics in this process; however, the local abundance of a fished site was reduced before the next unit of effort was allocated. The result of one unit of effort was a fishing mortality of 0.05 within the site. This value represented exploitation at a small spatial scale where a single trawl could substantially reduce local abundance.

The choice of fishing site was modeled as either completely random or a selective process. In the random case, each site was assigned an equal probability drawn from a uniform distribution between zero and one. The random number was then compared with a sequential sum of the probabilities among the sites. When the sum was less than the random number, the site index was incremented. When the sum equaled or exceeded the random number, the previously indexed site was selected. For example, if the first three sites had probabilities 0.0020, 0.0010, and 0.0030 and the random number 0.0021 was chosen, then the second site would be selected. Selective fishing employed a similar algorithm. However, the initial site probabilities were related to the abundance of fish at the site (N_i) and rescaled to sum to one:

$$(2) \qquad P(\text{site}_i) = \frac{N_i^{\theta}}{\sum_i N_i^{\theta}}$$

where θ is the exponent of selectivity. When $\theta = 0$, all sites had equal probability of being selected, i.e., effort allocation was completely random. With $\theta = 1$, probabilities were directly proportional to abundances but still stochastic. Increasing θ disproportionately increased the probability of selecting sites of high abundance, approaching a limit where the site with the highest abundance is always the next site exploited: deterministic site selection. A $\theta = 4$ was chosen to strongly favor the selection of sites with high abundance but still allow some stochasticity in fishing activities. The range of site probabilities varied between 2.30×10^{-8} and 0.003, with approximately 0.8% of the probabilities greater than 0.001.

Three cases were examined: (*i*) random fishing, (*ii*) selective fishing, and (*iii*) selective fishing with high effort (intensive fishing). For each case, 100 simulated fishing seasons were used to define the range of skews observed in the catch rate distributions. The $\log_{10}$-transformed catch rates were examined through boxplots of the distribution of skews among all 100 simulations. Throughout this paper, skew was calculated from the third moment of the statistical distribution of the catch rates:

$$(3) \qquad \text{skew} = \frac{\frac{1}{N}(x_i - \bar{x})^3}{\left(\frac{1}{N}(x_i - \bar{x})^3\right)^{\frac{3}{2}}}$$

where N is the sample size, x_i are the observations, and $\bar{x}$ is the sample mean (Joanes and Gill 1998). Algorithms were developed in R (R Development Core Team 2005) and recoded in ANSI C to speed up execution. Random number generation in C was performed using the routines from Numerical Recipes in C (Press et al. 2002).

Data from the Dutch beam trawl fishery

Records of the fishing activities for beam trawlers of Dutch registry were reported by commercial fishers and were available through IMARES (Wageningen Institute for Marine Resources and Ecosystem Studies, IJmuiden, Netherlands). Information was available as daily accounts of the location fished (ICES rectangle, see Fig. 1) and the landed weight of the species caught. These landed catches were the equivalent of a catch rate (catch per unit effort) where the unit of effort was one day. We examined records from 1998 to 2003. Our analysis focused on species that were present in over 1% of the landed weight of the entire fishery: brill (*Scophthalmus rhombus*), Atlantic cod (*Gadus morhua*), dab (*Limanda limanda*), European flounder (*Platichthys flesus*), lemon sole (*Microstomus kitt*), Norway lobster (or nephrops, *Nephrops norvegicus*), plaice (*Pleuronectes platessa*), rays and skates (*Raja* spp.), sole (*Solea solea*), turbot (*Psetta maxima*), and whiting (*Merlangius merlangus*).

The value of the species examined was determined from annual summaries of auctions published by Dutch Fish Product Board (P.O. Box 72 2280 AB Rijswijk, Netherlands) in most cases. To obtain a complete set of prices for nephrops, we used additional price information published by the European Commission's Directorate-General for Fisheries and Maritime Affairs (B-1049 Brussels, Belgium) for 1998 and 1999. Skates and rays were excluded from the eco-

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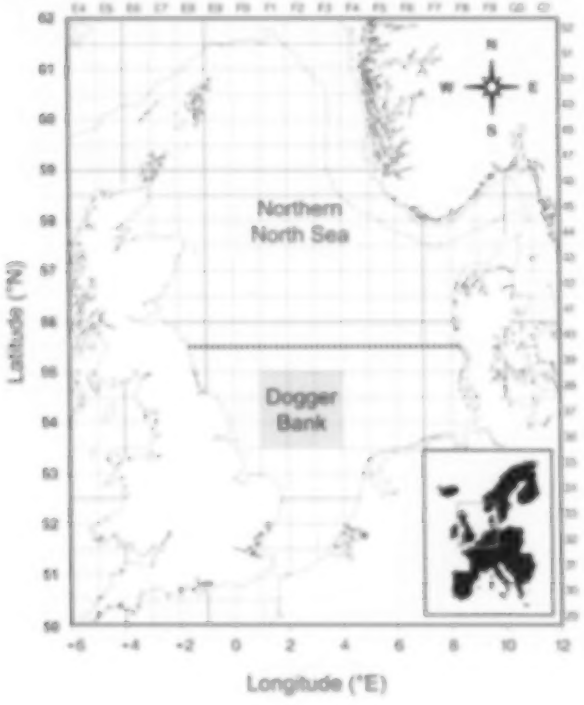
Fig. 1. Map of the North Sea. Values displayed at the top and on the right of the map are ICES rectangle coordinates. The shaded area indicates the ICES rectangles associated with the Dogger Bank in this study. The broken line designates the boundary for the northern region as defined for our analysis.



nomic analysis because prices were not available from these sources for all of the years examined.

Data from the beam trawl catches of the research survey vessel (R/V) *Isis* were examined for comparison with the commercial fishery. These data were available for all of the years studied. Information on time, location fished, and species caught was recorded for each trawling action.

Analyses of fishery data

We introduced a graphical presentation to compare catch rate distributions among species, which we named the "delta plot" after Pennington's delta-lognormal distribution (Pennington 1983) for fisheries data. All non-zero catch rates were $\log_{10}$-transformed prior to examination to compare them more easily with the reference point of the lognormal distribution as in the previous simulation. Each species was represented by plotting the first letter of their common name at coordinates defined by the proportion of records where it was lacking (zeros) on the horizontal axis and the skew of the distribution of the transformed non-zero catch records on the vertical axis. A shaded circle was added to the symbol for those species whose skew was significantly different from zero according to the D'Agostino D test (Fig. 4). Ideally, a target species should be common in the catch and exhibit a large negative skew relative to other species caught, appearing in the lower left region of the delta plot.

The influence of prices on the fishery was examined by comparing them with both total landed weight and total landed value of the species caught. All of these were based on annual summaries for the 6 years studied. If price dominated targeting decisions, then the price structure should be closely correlated with the total landed value and the total landed weight of the species caught. Alternatively, higher weights and values for less profitable species would indicate that fishing activities are not directed by price alone.

The relationship between the economic data and the distribution of the catch rate data was examined by graphing the relationship between skews and total landed values among the species for each of the 6 years examined. Trends were defined by Pearson correlations, and their significance was tested using 500 randomizations of the data pairs (Manley 1997). Large total landed values corresponding to large negative skews would result from the postulated targeting influence on catch distributions.

Fleet sectors examined

The data from Dutch beam trawl fishery were studied in three separate analyses: (*i*) offshore vessels, (*ii*) eurocutters around the Dogger Bank, and (*iii*) offshore vessels in the northern North Sea. To avoid biases in our results caused by varying distributions of horsepower within the fleet, eurocutters were defined as vessels with 300 (±1%) horsepower and offshore vessels were defined as 2000 (±1%) horsepower. This reduced the number of records analyzed but still accounted for over half of the reported trips. Catch and economic indicators of targeting were examined for the offshore vessels fishing throughout the North Sea. These larger vessels were restricted from fishing in certain areas near the coasts, such as the "plaice box" on the Dutch, German, and Danish coasts (Pastoors et al. 2000). They employed mesh sizes of 80–100 mm and typically trawled at a speed of about 6 knots (Rijnsdorp et al. 2000*b*). They presented the largest aggregation of data from a uniform vessel class in this fishery and were thus well suited to analyses based on statistical distributions.

Dutch eurocutters typically focused their effort in coastal regions. Their smaller size corresponded to trawling speeds to 4 or 5 knots (Rijnsdorp et al. 2000*b*), but mesh sizes were drawn from the same range as the larger offshore vessels. However, in 1998, a small group of eurocutters within this fleet actively pursued nephrops around the Dogger Bank. We defined this region as ICES statistical reporting areas 36/F1, 36/F2, 36/F3, 37/F1, 37/F2, 37/F3, 38/F1, 38/F2, and 38/F3 (Fig. 1). These vessels produced 472 records of fishing around the bank. Their trips may represent exploratory fishing, but regardless of the cause, they were not repeated in subsequent years. This geographical division within the eurocutters provided an opportunity to test the ability of our methodology to detect two different targeting strategies within the same vessel class.

Offshore vessels in the northern North Sea (defined as north of 55°30′N) were examined to compare their targeting patterns with those observed throughout the entire North Sea. This boundary roughly corresponded to regulatory conditions in the fleet. Larger (100 mm) mesh was required north of 55°N, and in 2000, this was shifted to 56°N in the region east of 5°E. Specifically, we wanted to examine how

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Fig. 2. Skews in transformed simulated fish and catch distributions. Skews were calculated from the third moment of the $\log_{10}$-transformed distributions. The boxplots summarize the distribution of skews from 100 simulated fishing seasons. The circles represent points that are beyond 1.5 times the interquartile range.

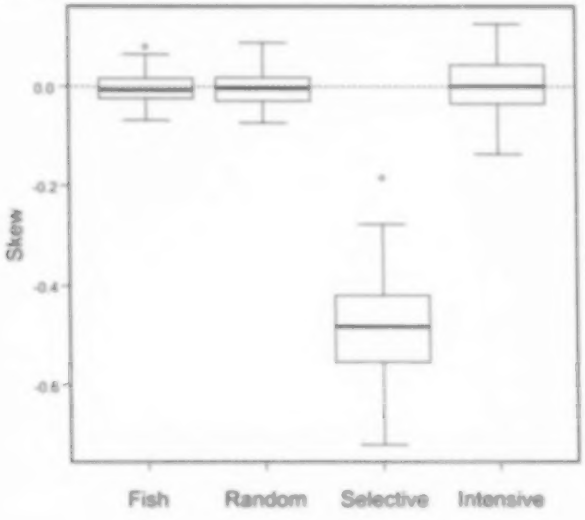
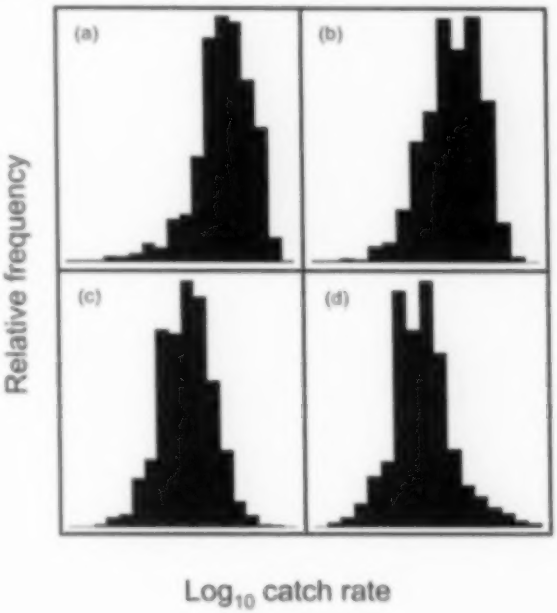


Fig. 3. The catch rate distribution of four species from the offshore beam trawl fleet in 2003. Each catch record represents one day of fishing within one ICES rectangle. The species illustrated are (*a*) sole (n = 23 383), (*b*) plaice (n = 25 528), (*c*) dab (n = 23 085), and (*d*) cod (n = 14 257).



a large reduction in sole availability would impact the observed catch distributions. Sole prefer the warmer waters that are more common coastally and in the south of the North Sea (Rijnsdorp and van Beek 1991; Horwood and Millner 1998; Poos and Rijnsdorp 2007). They are less common in the north and are less likely to provide an economically viable target. The key questions were (*i*) would the skew observed in sole catches change with changing sole availability, and (*ii*) would the skew of associated species such as plaice be affected by the reduction in sole?

The R/V *Isis* collected beam trawl samples throughout the eastern North Sea in the regions exploited by the Dutch fisheries. This survey was designed to focus on areas with higher catches of sole and plaice, so it cannot be considered completely random. However, fishing was randomized within sampling strata, reducing the potential effects of targeting at small spatial scales. The tonnage (181 tonnes), mesh size (40 mm), and towing speed (4 knots) were all less than those of commercial vessels. However, the distribution of catch rates for research vessels still provided insight into skews in comparison with those of the commercial fleet. The number of trawls made by a single research vessel during a year (<100) was significantly less than those examined in the commercial fleet components. Therefore only the catch rate distributions of the three most common species (sole, plaice, and dab) were examined.

Results

The simulation model

In our simulation, the presence of site selectivity generated a negative skew in the transformed catch rates that was not present in the original fish abundances. The distribution of skews generated by random fishing, selective fishing, and intensive fishing are illustrated (Fig. 2). Random fishing, like random sampling, generated little variation from the shape of the original lognormal distribution. Alternatively, selective fishing resulted in a noticeable negative skew in the transformed catches. However, this bias was reduced and, in some cases, lost when the amount of fishing effort increased (intensive fishing with selectivity). In this case, the potential effectiveness of selective fishing was reduced by reducing local abundances in the best sites and spreading fishing activities more evenly among sites.

The offshore beam trawl fleet

A variety of distributions were observed among the species caught in the offshore fleet. The profiles of the log-transformed catch rates (Fig. 3) show both sole and plaice displaying negative skews relative to the lognormal distribution. Cod displays a positive skew, and dab shows near symmetry. All four of these species were common in catch records (>75%) and were often caught together.

The skew of the $\log_{10}$-transformed catch for each species in the offshore fleet is usually statistically different from zero (Fig. 4). The D'Agostino D test was able to detect small departures from the lognormal because of the large number (greater than 10 000 in each year) of records available to define catch rate distributions in the offshore fleet. Generally, the greatest negative skews occur among some of those species that appear commonly in the catch (>80% of the records). However, these common species display a range of skews, including some relatively small positive ones. Less

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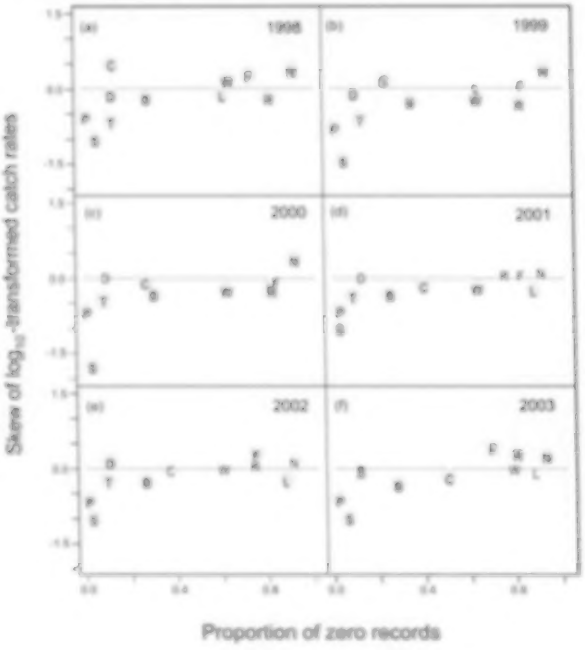
Fig. 4. Skew–zero plot of daily catch records for the North Sea Beam trawl fishery. Species are represented by the first letter of their common names: brill, cod, dab, flounder, lemon sole, Norway lobster, plaice, sole, turbot, and whiting. Zeros represent the proportion of daily records within a trip that do not have entries for the species examined. Skews are calculated from the third moment of the $\log_{10}$-transformed positive catch values of the species. Statistically significant skews (D'Agostino's D test, $p < 0.05$) are indicated by a shaded circle around the letter. Total number of records used to calculate skew and proportions for each year: (*a*) n = 31 036 (1998), (*b*) n = 30 198 (1999), (*c*) n = 41 523 (2000), (*d*) n = 30 423 (2001), (*e*) n = 27 610 (2002), and (*f*) n = 26 815 (2003).



common species display smaller skews on either side of the expectation of zero.

In all of the years examined, sole and plaice display the largest negative skews (Fig. 4). This is consistent with effort being strongly directed toward them in this fishery. However, the magnitudes of their skews vary among the 6 years examined. In contrast, cod displays a positive or near-zero skew throughout the time period, which was expected for a species that is not being targeted or is possibly even being avoided.

Sole and plaice are not the most highly priced species landed in the fishery. Turbot had a higher price than sole in all of the years studied except 2001. In 1999, both turbot and brill were more highly priced than sole. We summarize the range of prices, total landed weights, and total landed values for those species for which financial data were available throughout the study period (Fig. 5). It is clear that plaice dominates the landed weight, whereas sole dominates the landed value. The other species, the prices of which were both greater and less than these two, appear less important in the landed catch. This pattern appears stable throughout the

Fig. 5. The relationship between (*a*) landed weight and (*b*) landed value and price for the species studied in the offshore fleet. Each species is represented by the first letter of its common name (brill, cod, dab, flounder, lemon sole, nephrops, plaice, sole, turbot, and whiting) for each of the six years studied (1998–2003).

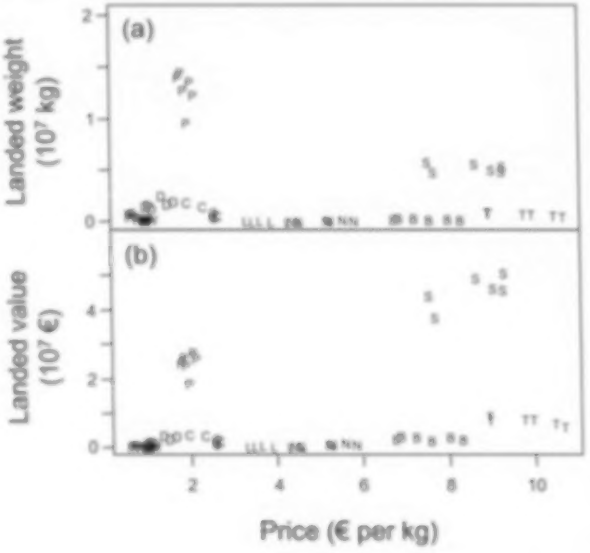
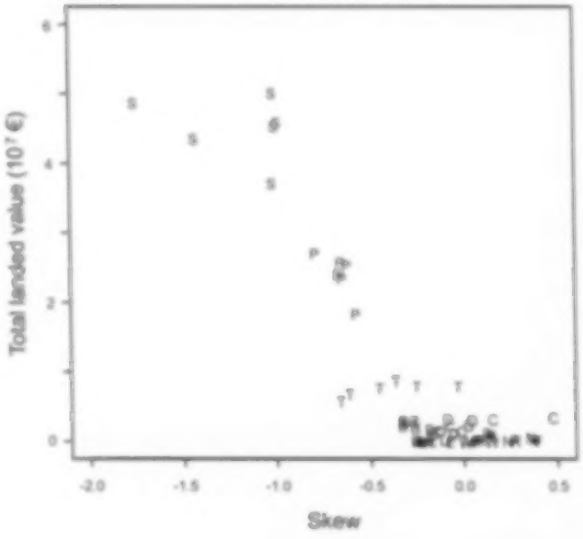


Fig. 6. The relationship between skew and total landed value in the catch of the offshore beam trawls for each of the six years studied (1998–2003). The annual values for each species are represented by the first letter of their common name (brill, cod, dab, flounder, lemon sole, nephrops, plaice, sole, turbot, and whiting).



period studied. Spearman rank correlations indicated that there was no relationship between price and landed weight ($p > 0.60$ for all years) and only a weak relationship between

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price and landed value in one of the years examined (2001, $r_S = 0.67$, $p = 0.04$).

There was a negative relationship between skew and total value of the species landed (Fig. 6). Randomization tests showed that this relationship is statistically significant ($p < 0.01$) in all of the 6 years studied. The trend was clearest among the species with the highest landed values (sole, plaice). However, the relationship became more poorly defined among less economically important species (Fig. 6, right-hand side), the skew of which typically departed from the symmetry of the theoretical lognormal by less than 0.5. Sole showed much more variability than plaice in this figure. The three points of sole that illustrated high total landed value and relatively small negative skew corresponded to the three later years of the study (2001–2003).

Eurocutters on Dogger Bank

In 1998, the aggregated data from all eurocutters displayed patterns similar to those of the offshore fleet, with the exception of one species: nephrops (Fig. 7*a*). Nephrops was relatively rare in the catch of this fleet component but clearly displayed the strong negative skew that we associate with targeting. When eurocutters fishing around Dogger Bank were examined in isolation, the general pattern observed in the offshore fleet returned, but with nephrops appearing at the lower left of the graph rather than sole and plaice (Fig. 7*b*). Economically, nephrops made up 67% of the landed value of eurocutters on Dogger Bank. Cod had the next largest landed value, but this was only 11%. Each of the remaining species contributed less than 10% to the total landed value of this fleet component. Thus both the catch rate distribution and economic data support nephrops as a target in this subset of the eurocutters.

The offshore fleet in the northern North Sea

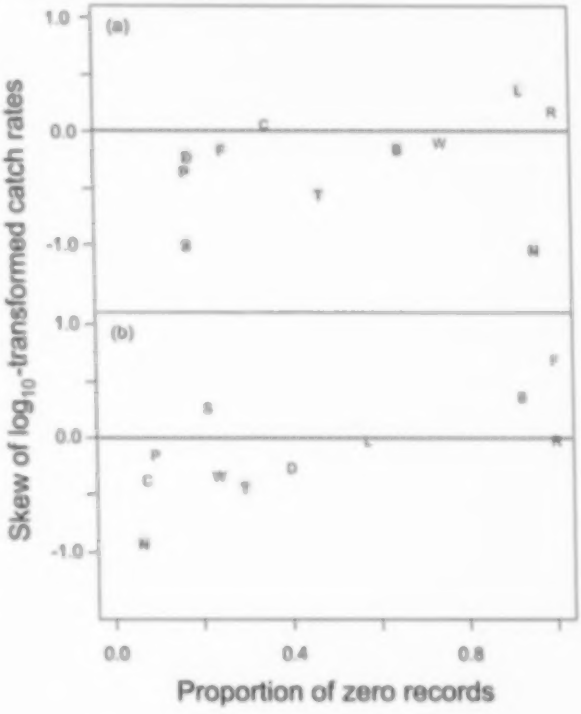
North of 55°30′N, the pattern formed by skews and zeros from offshore vessels appears superficially similar to that of the entire fleet (Fig. 8). However, sole is less common in the catch and no longer possesses an extreme negative skew. Plaice displays the greatest negative skew in all years, with the exception of 2003 when dab displayed a similar skew.

Economically, the contribution of sole in this area varied from 20% of the landed value in 2000 to only 6.5% in 2003. Plaice was the most important species economically, making up over 50% of the total landed value in all of the years studied, with a maximum of 74% in 2003. It was also the most common in the records for all of the years examined.

Survey trawls by the R/V *Isis*

The distribution of the logarithm of sole and plaice catch rates in the survey trawls did not show significant deviation from symmetry (Table 1). The power to detect such changes was reduced because of sample sizes that were small relative to those of the commercial data. However, the magnitude of the observed skews was also less than observed in the commercial data. In contrast, dab displayed a significant negative skew in the survey data during the last three years that was not apparent in the commercial data or the first three survey years examined. During 2001–2003, the log-transformed catch rates of dab were significantly correlated with depth, increasing in deeper waters. However, this trend was not observed in the R/V *Isis* survey data during the earlier years, nor was it seen in sole or plaice in any of the years surveyed. Survey trawl depths ranged from 13 to 55 m, with approximately 90% of the trawls made in waters deeper than 20 m during the years studied.

Fig. 7. The skew–zero plot for the eurocutters fishing in 1998 (*a*) in all areas and (*b*) only in those ICES rectangles in the offshore area around the Dogger Bank. Species are represented by the first letter of their common names: brill, cod, dab, flounder, lemon sole, Norway lobster, plaice, sole, turbot, and whiting. Statistically significant skews (D'Agostino's D test, $p < 0.05$) are indicated by a shaded circle around the letter.



Discussion

The role of sole and plaice as target species in the Dutch beam trawl fishery is reflected both statistically and economically in the landings. Both measures highlight sole in the offshore fleet as the most economically important species and the species that displays the greatest deviation from the skew expected for a lognormal distribution. Plaice is also important, being most common in the catch and possessing large negative skews and high total landed values. But is plaice a target species? Recent analyses show that the partial F values of sole and plaice in the North Sea are correlated at some times and unrelated at others (Rijnsdorp et al. 2006). It is theoretically possible for an abundant species that is closely associated with a target species to dominate the landed weight, even when effort is not directed toward it. This will be difficult to resolve when the more valuable species cannot be profitably caught independently of the other. However, the landings have shown that plaice is clearly a target for at

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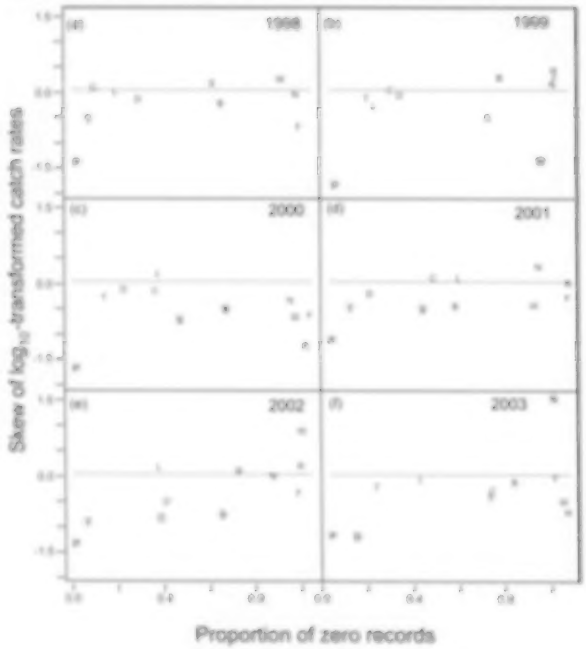
Fig. 8. The skew–zero plot of offshore beam trawl catches from the northern North Sea for each of the 6 years studied. Species are represented by the first letter of their common names: brill, cod, dab, flounder, lemon sole, Norway lobster, plaice, sole, turbot, and whiting. Statistically significant skews (D'Agostino's D test, $p < 0.05$) are indicated by a shaded circle around the letter.



least part of the offshore fleet. In the northern North Sea where sole is less common, plaice possesses both the greatest total landed value and the largest negative skew. The reduced availability of sole is reflected by its reduced appearance in the catch and a skew that is typical of other nontarget species.

Price alone is a poor indicator of economic importance. Sole does not have the highest price, and the price of plaice is typical of other low-valued groundfish. Price reflects market potential, but not fishing potential. The abundance and distribution of species will influence their availability and combine with prices to determine the most profitable target species. The total landed value of a species is the most direct measure of its economic importance in a fishery, trip, or set. The identification of targeting by landed weight is common in the "quantification levels" used by many agencies and described by Biseau (1998) but neglects the fundamental currency that directs industrialized fishing. Weight alone would make plaice appear more important than sole in this offshore fleet, which contradicts the relationship indicated by their total landed values.

The example of sole and plaice illustrates how close ecological associations among species will make it difficult to identify the "true" target species using any statistical methodology. Ideally, areas where the species are not in association can be used to investigate the issue. In the offshore North Sea fleet, the apparent targeting of both sole and

Table 1. Skews in $\log_{10}$-transformed catch rate distributions by the R/V *Isis* during the annual Dutch beam trawl survey.

Year	Zeros	Skew	n	p[skew]
(*a*) Sole (*Solea solea*)				
1998	0.10	–0.320	63	0.461
1999	0.07	–0.171	87	0.646
2000	0.14	–0.126	78	0.745
2001	0.17	+0.005	58	0.990
2002	0.13	–0.117	77	0.764
2003	0.17	–0.373	71	0.369
(*b*) Plaice (*Pleuronectes platessa*)				
1998	0.01	+0.473	69	0.267
1999	0.01	+0.675	93	0.082
2000	0.01	–0.529	90	0.168
2001	0.00	+0.133	70	0.744
2002	0.02	+0.186	87	0.617
2003	0.00	–0.076	86	0.837
(*c*) Dab (*Limanda limanda*)				
1998	0.01	0.212	69	0.608
1999	0.01	–0.134	94	0.708
2000	0.01	–0.677	90	0.168
2001	0.00	–1.632	69	0.002
2002	0.02	–1.464	88	0.001
2003	0.00	–0.996	81	0.023

plaice may be confounded. However, north of 55°30′N, where sole is less abundant, plaice are common in the catch and possess the largest negative skews. Thus, this species can be a target on its own, despite its low price. The loss of sole as a target species in the north illustrates the importance of both the availability at sea and the price on shore in fisher's decisions.

The relationship between reported landings and catch on the water is an important concern in any analysis of commercial data, especially when quotas may limit the landings of some species. Anecdotal information from the fishing industry indicates that high-grading occurs under exceptional conditions in the Dutch beam-trawl fishery but is not a general phenomenon. Quirijns et al. (2007) showed that fishers can avoid high-grading by choosing fishing grounds that match the relative fishing rights for sole and plaice. Thus, we consider that the impact of high-grading on our analysis is minimal.

The delta plots introduced in this paper effectively summarize potential targeting biases in the landings data. The frequency of zeros in the data provides a clear indication of occurrence, and the skew of log-transformed catch rates differentiates among commonly occurring species. Negative skews are consistent with preferential fishing in areas of high-abundance, skews near zero suggest the incidental catch of a ubiquitous species, and positive skews in the landed catch suggest avoidance (or possibly high-grading) of a species with a restricted quota (e.g., cod). Generally, we expect to see a "dog-legged" pattern in these plots, with rarely caught species grouped around a skew of zero on the right and a range of skews between low positive and high negative values on the left. The presence of several distinct

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targeting strategies within the same data can result in low occurrences with relatively high negative skews, as was observed with nephrops in the small vessel fleet.

Not all deviations in skew will be the result of targeting or avoidance. In addition to statistical significance, the relative skews among all species simultaneously caught should also be considered. Only species with the most extreme, statistically significant, negative skews should be postulated as targets. These deviations may also reflect the applicability of the lognormal as a reference point for the distribution of fish among alternative sites. For example, the distribution of site quality may constrain the distribution of fish so that the lognormal does not strictly apply. The fishing history from previous seasons may also impact the initial distribution of abundances among sites. Finally, small deviations from symmetry in the log-transformed catch rates will often be detectable because of the large number of records present in many fisheries data sets. This could generate confusion if each significant result is interpreted without regard to the range of skews observed among the species caught.

Relatively large, significant skews may arise from interactions between trawl locations and biological distributions without deliberate targeting. Large negative skews in the *Isis* survey were seen for dab when their log-transformed catch rates increased with depth. The distribution of trawling effort in the survey design, favoring depths over 20 m, resulted in a large number of high-abundance hauls and a few shallow-water hauls with low abundances. When there was no relationship between depth and catch rate, the dab skews were smaller and not statistically significant. Thus, from 2001 to 2003, the survey design unintentionally "targeted" dab by placing more effort at depths where they occurred in high abundance.

The sample sizes from a single survey vessel are much less than those available from commercial fleets. However, they represent a valuable contrast to economically directed commercial effort. In our study, the *Isis* survey's skews for sole and plaice were relatively low and not statistically significant. This was consistent with a randomized survey that does not direct effort to maximize catch rates. Furthermore, the significant skews of dab during the last three years of this study, discussed above, illustrated that the sample sizes were high enough to detect large skews similar in magnitude to those observed in the commercial data.

Our simulation model suggests that when all possible fishing locations are being exploited, the targeting bias in catch distributions will be reduced or even eliminated. A reduction in skew accompanying obvious increases in fishing activities would suggest that the fishery has become "spatially saturated", especially if the economic contribution of the species remains high. Conceptually, this differs from "habitat saturation" in the ecological literature (Brown 1978; Emlen 1982) because of the lack of strict territoriality among foragers. The appearance of a spatially saturated fishery would imply that all accessible habitat used by a species is being regularly fished. Spatial saturation could contribute to stock contractions by placing pressure in areas that could otherwise serve as low-abundance refuges for the exploited species. In combination with habitat selection effects (MacCall 1990; Swain and Wade 1993), it could lead to more extreme stock contractions by eliminating the stock components in marginal regions more quickly. Monitoring skews and effort among years could aid managers tracking the growth of developing fisheries. The declining skews of sole associated with large total landed values over the last three years studied suggest that spatial saturation may be increasing with this species.

The fishing mortalities in our simulation model vary greatly from those determined for plaice and sole by Rijnsdorp et al. 2006. They estimated F per vessel per day as 1.0×10^{-5} for sole and 0.6×10^{-5} for plaice as opposed to the 5.0×10^{-2} used in our simulation. However, their F is calculated across the entire population, whereas our parameter is restricted to the effects in a small (1/10 000) spatial component of the fishery. Furthermore, the overall patterns generated by the simulation will be robust to declines in F as long as the amount of effort is increased correspondingly.

Log-transformed catch rates may lack symmetrical distributions because, unlike our simulation, the underlying fish distribution may not be lognormal. Catch rate distributions that are not lognormal are often observed (Myers and Pepin 1990) but the underlying distribution of fish is usually not known. Our simulation could easily be repeated with the fish distributions represented by another skewed distribution, such as a gamma, that can generate negative skews in log-transformed data. In the context of our simulation, this would center the skews from random fishing around a negative value rather than zero. However, this would not change the tendency for selective fishing to create even stronger negative skews in the log-transformed catch rates.

The selective fishing of sites with high local abundances results in a reduction in the relative representation of the large catch rates in the catch data. Though this may initially seem counterintuitive, it results from the repeated exploitation of high-abundance sites, reducing them to lower-abundance sites as the fishery progresses. Thus, selective behavior will erode the right-hand side of both the distribution of observed catch rates and the distribution of the log-transformed catch rates. This erosion will shift the balance of the distribution away from the right and result in more negative skews than would be experienced with random fishing. The key to generating this effect is not the specific underlying distribution of fish, but the ability of fishers, through knowledge and choice, to consistently select sites that yield above-average catch rates from among those sites that are available.

Previous attempts to quantify targeting have focused on individual trips or sets rather than aggregated data across fleet sectors or areas. The goal was usually to select subsets of data for use in stock assessments and management (Biseau 1998; Alemany and Álvarez 2003; Mahévas et al. 2004). Examining the distribution of catch rates is not a replacement for these methods, but a complement. Our analysis provides a rapid overview of entire fisheries or fisheries sectors that can be compared with the results of these other methods. The patterns of skews and zeros in the subsets of fishing trips can be used to examine their homogeneity and support the identity of hypothesized target species. A lack of skew combined with dominance in landed quantity and value would suggest spatial saturation within the fleet subset being examined and warrant closer examination.

"Quantification level" is a common method for classifying trips or sets for use in stock assessments (Ketchen 1964;

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Biseau 1998). It identifies the target species within catches from individual sets based on their landed weight exceeding a threshold proportion. In the offshore North Sea fleet, this would favor plaice as a target species, even though sole yielded the greatest landed value. If the quantification level threshold were set high enough (>25%), sole would not even be identified as a target. The skews of catch rate distributions may also be misleading. Strong associations among species may result in extreme negative skews in species that are not pursued. This will raise questions about the ecological and technological relationships among the species landed, but it will not overlook possible targets.

Multivariate methods can identify associations among species, areas, and other variables in commercial catch data (Pelletier and Ferraris 2000; Holley and Marchal 2004). In stock assessment, they are often used to classify trips or sets according to these variables. They form an important tool in the study of multispecies fisheries that can incorporate economic data (Lewy and Vinther 1994) and detailed geographic information (Branch et al. 2005). However, all multivariate methods can be sensitive to underlying assumptions, such as multivariate normality in the application of principal component analysis (PCA). Examining the distribution of catches within fishery components identified by these methods can both test the assumptions of multivariate methods and provide an additional means of evaluating the robustness of their performance when these assumptions are violated. Furthermore, the skews of these distributions can provide insights into the relative importance of different species in the targeting behavior within trips that are classified together.

The results of our simulation and analyses indicate that the assumptions of linear and generalized linear models that underlie many catch rate standardizations (Maunder and Punt 2004) can easily be violated. Changes in targeting behavior in response to variations in abundance or market conditions will result in error distributions that change in form over time or between regions. There is no simple solution to this problem. Mean–variance relationships within data are easily dealt with through transformation or the application of generalized linear models based on the appropriate link function and error distribution. In contrast, the variations in skew discussed here are a result of external factors, such as economics, that bias fishing activities. At the very least, deviations in error structure among the years or groups being compared should be investigated.

Deviations from Pennington's (1983) delta-lognormal distribution, commonly observed in current fisheries analyses, can provide useful information about patterns of species exploitation in a multispecies commercial fishery. They can be applied in conjunction with economic data or when economic data is not readily available. The relative value of the deviations among all species caught should be examined in addition to comparisons to the delta-lognormal, which may be misleading when the underlying fish distribution does not follow the lognormal. Thus, extreme negative skews associated with commonly caught species in a multispecies fishery suggest targeting but are not definitive; additional evidence should be examined. Any deviations caused by targeting behavior may be lost when fishing intensity increases, providing managers with an indication of how effort is distributed among potential fishing locations. In spite of these caveats, the patterns in catch rate, economic, and survey data observed in this North Sea fishery demonstrate that checking for these deviations can be informative. In the past, the mean and variance of catch distributions have received much attention in fisheries analysis. However, these are just two aspects of a distribution. We have illustrated that the third moment of these distributions is relevant beyond a statistical perspective; it relates to the underlying processes of fleet dynamics (sensu Hilborn 1985).

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References

Aitchinson, J. 1955. On the distribution of a positive random variable having a discrete probability mass at the origin. J. Am. Stat. Assoc. **50**: 901–908.

Alemany, F., and Álvarez, F. 2003. Determination of effective fishing effort on hake *Merluccius merluccius* in a Mediterranean trawl fishery. Sci. Mar. **67**: 491–499.

Bannerot, S.P., and Austin, C.P. 1983. Using frequency distributions of catch per unit effort to measure fish-stock abundance. Trans. Am. Fish. Soc. **112**: 608–617.

Biseau, A. 1998. Definition of a directed fishing effort in a mixed-species trawl fishery, and its impact on stock assessments. Aquat. Living Resour. **11**: 119–136.

Biseau, A., and Gondeaux, E. 1988. Apport des méthodes d'ordination en typologie des flotillas. J. Cons. Int. Explor. Mer, **44**: 286–296.

Branch, T.A., Hilborn, R., and Bogazzi, E. 2005. Escaping the tyranny of the grid: a more realistic way of defining fishing opportunities. Can. J. Fish. Aquat. Sci. **62**: 631–642.

Brown, J.L. 1978. Avian communal breeding systems. Annu. Rev. Ecol. Syst. **9**: 123–155.

Candy, S.G. 2004. Modelling catch and effort using generalized linear models, the Tweedie distribution, random vessel effects, and random stratum-by-year effects. CCAMLR Sci. **11**: 59–80.

Emlen, S.T. 1982. The evolution of helping. I. An ecological constraints model. Am. Nat. **119**: 29–39.

Halley, J., and Inchausti, P. 2002. Lognormality in ecological time series. Oikos, **99**: 518–530.

Hilborn, R. 1985. Fleet dynamics and individual variation: why some people catch more fish than others. Can. J. Fish. Aquat. Sci. **42**: 2–13.

Hilborn, R., and Mangel, M. 1997. The ecological detective: confronting models with data. Princeton University Press, Princeton, New Jersey.

Hilborn, R., and Walters, C.J. 1992. Quantitative fisheries stock assessment. Chapman and Hall, Inc., New York.

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Holley, J.-F., and Marchal, P. 2004. Fishing strategy development under changing conditions: examples from the French offshore fleet fishing in the North Atlantic. ICES J. Mar. Sci. **61**: 1410–1431.

Horwood, J.W., and Millner, R.S. 1998. Cold induced abnormal catches of sole. J. Mar. Biol. Assoc. U.K. **78**: 345–347.

Joanes, D.N., and Gill, C.A. 1998. Comparing measures of sample skewness and kurtosis. Statistician, **47**: 183–189.

Johnson, N.L., and Kotz, S. 1970. Continuous univariate distributions. 1. Distributions in Statistics. John Wiley, New York.

Ketchen, K.S. 1964. Measures of abundance from fisheries for more than one species. Rapp. P.-V. Reun. Comm. Int. Explor. Mer, **155**: 113–116.

Kimura, D.K. 1981. Standardized measures of relative abundance based on modeling log(c.p.u.e.), and their application to Pacific ocean perch (*Sebastes alutus*). J. Cons. Int. Explor. Mer, **39**: 211–218.

Lewy, P., and Vinther, M. 1994. Identification of Danish North Sea trawl fisheries. ICES J. Mar. Sci. **51**: 263–272.

MacCall, A.D. 1990. Dynamic geography of marine fish populations. University of Washington Press, Seattle, Washington.

Mahévas, S., Sandon, Y., and Biseau, A. 2004. Quantification of annual variations in fishing power due to vessel characteristics: an application to the bottom-trawlers of South-Brittany targeting anglerfish (*Lophius budegassa* and *Lophius piscatorius*). ICES J. Mar. Sci. **61**: 71–83.

Manley, B.F.J. 1997. Randomization and Monte Carlo methods in biology. 2nd ed. Chapman and Hall, New York.

Maunder, M.N., and Punt, A.E. 2004. Standardizing catch and effort data: a review of recent approaches. Fish. Res. **70**: 141–159.

McCullagh, P., and Nelder, J.A. 1989. Generalized linear models. 2nd ed. Chapman and Hall, New York.

Myers, R.A., and Pepin, P. 1990. The robustness of lognormal-based estimates of abundance. Biometrics, **46**: 1185–1192.

Pastoors, M.A., Rijnsdorp, A.D., and Van Beek, F.A. 2000. Effects of a partially closed area in the North Sea (plaice box) on stock development of plaice. ICES J. Mar. Sci. **57**: 1014–1022.

Poos, J.-J., and Rijnsdorp, A.D. 2007. The dynamics of small-scale patchiness of plaice and sole as reflected in the catch rates of the Dutch beam trawl fleet and its implications for the fleet dynamics. J. Sea Res. **58**: 100–112.

Power, J.H., and Moser, E.B. 1999. Linear model analysis of net catch data using the negative binomial distribution. Can. J. Fish. Aquat. Sci. **56**: 191–200.

Pelletier, D., and Ferraris, J. 2000. A multivariate approach for defining fishing tactics from commercial catch and effort data. Can. J. Fish. Aquat. Sci. **57**: 51–65.

Pennington, M. 1983. Efficient estimators of abundance, for fish and plankton surveys. Biometrics, **39**: 281–286.

Press, W.H., Teukolsky, S.A., Vetterling, W.T., and Flannery, B.P. 2002. Numerical recipes in C: the art of scientific computing. 2nd ed. Cambridge University Press, New York.

Quinn, G.P., and Keough, M.J. 2002. Experimental design and data analysis for biologists. Cambridge University Press, New York.

Quirijns, F.J., Poos, J.J., and Rijnsdorp, A.D. 2007. Standardizing commercial CPUE data in monitoring stock dynamics: accounting for targeting behaviour in mixed fisheries. Fisheries Research. doi:10.1016/j.fishres.2007.08.016.

R Development Core Team. 2005. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rijnsdorp, A.D., and van Beek, F.A. 1991. Changes in growth of plaice *Pleuronectes platessa* (L.) and sole *Solea solea* (L.) in the North Sea. Neth. J. Sea Res. **27**: 441–457

Rijnsdorp, A.D., van Maurik Broekman, P.L., and Visser, E.G. 2000*a*. Competitive interactions among beam trawlers exploiting local patches of flatfish in the North Sea. ICES J. Mar. Sci. **57**: 894–902.

Rijnsdorp, A.D., Dol, W., Hoyer, M., and Pastoors, M.A. 2000*b*. Effects of fishing power and competitive interactions among vessels on the effort allocation on the trip level of the Dutch beam trawl fleet. ICES J. Mar. Sci. **57**: 927–937.

Rijnsdorp, A.D., Daan, N., and Dekker, W. 2006. Partial fishing mortality per fishing trip: a useful indicator of effective fishing effort in mixed demersal fisheries. ICES J. Mar. Sci. **63**: 556–566.

Salas, S., Sumaila, U.R., and Pitcher, T. 2004. Short-term decisions of small-scale fishers selecting alternative target species: a choice model. Can. J. Fish. Aquat. Sci. **61**: 374–383.

Salthaug, A., and Godo, O.R. 2001. Standardization of commercial CPUE. Fish. Res. **49**: 271–281.

Smit, W. 1996. An economic approach to measuring fishing effort: application to a Dutch cutter fleet. Mar. Resour. Econ. **11**: 305–311.

Stocker, M., and Fournier, D. 1984. Estimation of relative fishing power and allocation of effective effort, with catch forecasts, in a multispecies fishery. Int. North. Pac. Fish. Comm. Bull. **42**: 3–9.

Swain, D.P., and Wade, E.J. 1993. Density-dependent geographic distribution of Atlantic cod (*Gadus morhua*) in the southern Gulf of St. Lawrence. Can. J. Fish. Aquat. Sci. **50**: 725–733.

Taylor, C.C. 1953. Nature of variability in trawl catches. Fish. Bull. **54**: 145–166.

Ulrich, C., and Andersen, B.S. 2004. Dynamics of fisheries, and the flexibility of vessel activity in Denmark between 1989 and 2001. ICES J. Mar. Sci. **61**: 308–322.

Weisterheim, S.J., and Foucher, R.P. 1985. Relative fishing power for Canadian trawlers landing Pacific cod (*Gadus macrocephalus*) and important shelf cohabitants from major offshore areas of western Canada, 1960–81. Can. J. Fish. Aquat. Sci. **42**: 1614–1626.

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Retention, breakdown, and biological utilisation of deciduous tree leaves in an estuarine tidal flat of southwestern British Columbia, Canada

Takashi Sakamaki and John S. Richardson

Abstract: In an estuarine mudflat connected to a mountainous stream, coarse leaf material from deciduous trees was examined for its utilisation by invertebrates, retention, and breakdown rate. Leaves from the stream were deposited in the upper intertidal parts near the stream mouth. Their standing stocks were high in fall (~23.8 g AFDM·m^{-2}) and mostly disappeared by spring. Breakdown rates of red alder leaf packs were higher at subtidal and lower intertidal stations (k = 0.013–0.027·day^{-1}) than at stream channel and upper intertidal stations (k = 0.006–0.009·day^{-1}). Longer contact of leaves with relatively warmer seawater may have enhanced leaf breakdown by microbial activities. In the upper intertidal stations, the decrease in the amount of deposited leaves from fall to spring (k = 0.023–0.039·day^{-1}) was faster than leaf breakdown in the leaf packs, thus physical export was probably significant in the decrease in deposited leaves. Meanwhile, amphipods dominated the invertebrates colonising leaf packs. The invertebrate densities did not significantly differ between natural and polyester leaf packs, suggesting contribution of leaves as a microhabitat rather than a food source. The carbon and nitrogen stable isotope signatures of amphipods indicated that benthic microalgae were their primary food source regardless of natural or artificial leaf packs.

Résumé : Nous avons étudié les feuilles décidues de ligneux en termes d'utilisation par les invertébrés, de taux de rétention, et de vitesse de décomposition sur un plateau boueux estuarien connecté à un cours d'eau de montagne. Des feuilles apportées par le cours d'eau se déposent dans la zone intertidale supérieure près de l'embouchure. Leur biomasse est élevée en automne (~23,8 g AFDM·m^{-2}) et réduite à presque rien au printemps. La décomposition des paquets de feuilles d'aulnes rouges est plus rapide sur les stations subtidales et intertidales inférieures (k = 0,013–0,027·jour^{-1}) que dans le chenal du cours d'eau et les stations intertidales supérieures (k = 0,006–0,009·jour^{-1}). Le contact plus prolongé des feuilles avec l'eau de mer relativement chaude pourrait avoir activé la décomposition des feuilles via l'activité microbienne. Sur les stations intertidales supérieures, la réduction de la quantité de feuilles durant l'automne et le printemps (k = 0,023–0,039·jour^{-1}) est plus rapide que la décomposition des feuilles; l'exportation physique joue donc probablement un rôle significatif dans la réduction des feuilles accumulées. Les amphipodes dominent des assemblages d'invertébrés qui colonisent les paquets de feuilles. Les densités d'invertébrés ne diffèrent pas significativement dans les paquets de feuilles naturelles et les paquets de feuilles en polyester, ce qui laisse croire que les feuilles sont utilisé comme un microhabitat plutôt qu'en tant qu'une source de nourriture. La composition en isotopes stables du carbone et de l'azote des amphipodes indiquent que ces animaux utilisent les algues microscopiques comme principale source de nourriture dans les paquets de feuilles naturelles et artificielles.

[Traduit par la Rédaction]

Introduction

Various materials, e.g., sediment, organic matter, and nutrients, are transported down through river systems (e.g., Wipfli et al. 2007), and parts of these fluxes are thought to be deposited and retained in estuaries because of their relatively low gradient. In estuaries, some studies applying stable isotope analyses showed that particulate organic matter (POM) from rivers dominated the organic matter in sediments and significantly contributed to diets of organisms (e.g., Thornton and McManus 1994; Chanton and Lewis 2002; Kasai and Nakata 2005). These studies indicate that POM from rivers can greatly affect chemical and biological features of estuaries. Meanwhile, the amount, origin, size, and chemical compositions of POM transported through rivers are expected to depend on characteristics of rivers such as riparian condition, watershed land use, geological features, and hydrological properties (e.g., Johnson and Covich 1997; Hein et al. 2003; Munson and Carey 2004). In the Pacific coastal ecosystem, there are many streams that flow through steep, forested areas and discharge directly into estuaries. Although this type of river is expected to transport

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substantial amounts of tree leaves to estuaries, the dynamics and biological contribution of them to estuarine ecosystems have not been well examined (Kochi and Yanai 2006).

Within stream ecosystems, it has been reported that leaves provided from deciduous trees enhance secondary productivity of stream invertebrates, and temporal and spatial variation in leaf supply greatly affects community structures (e.g., Richardson 1991; Wallace et al. 1997). Leaves were also experimentally shown to be used primarily as a food source for stream invertebrates, although some species likely used them as microhabitat (Richardson 1992*a*; Dudgeon and Wu 1999). In turn, feeding activities by stream invertebrates result in enhanced leaf decomposition; in particular, shredders contribute to leaf breakdown (e.g., Sponseller and Benfield 2001; Hieber and Gessner 2002). In streams, microbial activities by bacteria and fungi also contributes to leaf breakdown, which is largely controlled by extrinsic and intrinsic chemical factors such as nutrient concentration of ambient water and chemical composition of leaf (e.g., Robinson and Gessner 2000; Motomori et al. 2001). Physical fragmentation also accelerates leaf breakdown (Hill and Perrote 1995; Hoover et al. 2006).

Estuaries have environmental characteristics that differ from those of streams, potentially leading to unique dynamics of leaf litter from streams. Tidal submersion–emersion cycles in intertidal zones significantly affect the physical environment, e.g., bed shear stress, temperature, and water content of sediment (e.g., O'Brien et al. 2000; Uncles and Stephens 2000), and tidal exchanges of seawater and freshwater vary the chemical environment, e.g., salinity and nutrient concentration in water column and sediment (e.g., Kuwae et al. 2003; Sakamaki et al. 2006). Particularly in intertidal zones, these environmental factors are also expected to vary spatially with elevation because of differences in emersion time and water mixture rates. This may cause spatial differences in leaf dynamics along the bed gradient. As for leaf utilisation by organisms in estuaries, an experimental study by Kochi and Yanai (2006) suggested that amphipods used oak leaves mainly as a habitat. However, it is still unknown how environmental factors unique to estuaries affect leaf litter dynamics and biological utilisation.

Studies in streams have shown that leaf species is an important factor controlling its breakdown rate and feeding and colonisation by invertebrates (Canhoto and Graça 1996; Motomori et al. 2001; Richardson et al. 2004). In the northwest Pacific coast region, red alder (*Alnus rubra*) is a very common species of deciduous tree. Alder leaves, which have a relatively high nitrogen content, are known to have higher breakdown rates and be a better food source in comparison with leaves from other deciduous trees such as oak and chestnut (Canhoto and Graça 1996; Motomori et al. 2001; González and Graça 2003). In this study, we used alder leaves in an experiment as a representative species for our region and also as a species that might have stronger interactions with biological processes in estuaries.

We have focused on intertidal flats as a representative of estuarine depositional systems receiving terrestrial POM. The objectives of this study were to examine retention of deciduous tree leaves and their utilisation by organisms in an estuarine tidal flat. In particular, we addressed the following questions. (*i*) How long are leaves retained in the tidal flat? (*ii*) What controls the retention of leaves in the tidal flat? (*iii*) Which estuarine organisms use terrestrial leaves as food or habitat?

Materials and methods

Study sites

The estuarine tidal flat that we studied is at the inner end of an inlet (Port Moody Arm of Burrard Inlet) near Vancouver, British Columbia, Canada (49°17′N, 122°50′W) (Fig. 1). The main stream input to this estuary is from Noons Creek (about 0.3 $m^3 \cdot s^{-1}$, annual mean). This stream originates at 875 m elevation from a forested area and flows through the middle to lower reaches where riparian forest buffers are maintained in urbanised areas. The stream length and drainage area are about 11.5 km and 4.7 km^2, respectively. The maximum tidal amplitudes of this estuary in September and December 2004 were about 3.4 and 5.0 m, respectively. The elevations of the tidal flat area were estimated to range between about –2 and 1 m (from the mean water level in 2004). The tidal flat is predominated by muddy sediment, and average mud content and organic content of four points are 43% ± 12% and 4.9% ± 0.8% (mean ± standard error (SE), $n = 4$), respectively (T. Sakamaki and J.S. Richardson, unpublished data).

Investigation for standing stocks of leaves

The amount of deciduous leaves deposited (standing stock) on the tidal flat sediment surface was measured on 5 November 2004, 17 February 2005, and 10 May 2005. In the tidal flat, three transects (X, Y, Z) crossing the stream channel were set with intervals of about 100–200 m within the upper part of the tidal flat (Fig. 1). On each transect, three sampling plots of 2 m^2 were set at 20 m intervals. Samples were taken by thoroughly raking three times (rake with 2 cm pitches and 2 cm crooks) across the sediment surface of every plot. Collected leaves were washed on a 1 mm sieve in the brackish water on the site. In the laboratory, materials other than deciduous leaf, e.g., pieces of wood, coniferous leaves, seashells, and gravel, were removed by tweezers and dried at 60 °C for 48 h. Then the samples were analysed for organic matter amount based on dry mass loss during combustion (550 °C for 2 h).

Leaf pack experiment

A leaf pack experiment was conducted in the tidal flat to determine decomposition rates of red alder leaves and examine utilisation of leaves by estuarine invertebrates. Eighteen alder leaf packs were set at each of the stations A to F (Fig. 1). In addition, 18 polyester artificial leaf packs were set beside stations C and D (stations C-art and D-art). Station A was in the freshwater section of the stream and was not affected by tide. Stations B, C, and E were on the tidal flat, located about 30 to 50 m away from the stream channel. Station D was in the tidal channel of the stream. Station F was submerged all the time and the water depth was always >1 m. If invertebrates use leaf packs as habitat rather than as a food source, then we would predict that there should be no difference in the densities of invertebrates colonising the two types of leaf packs (Richardson 1992*a*). For natural leaf

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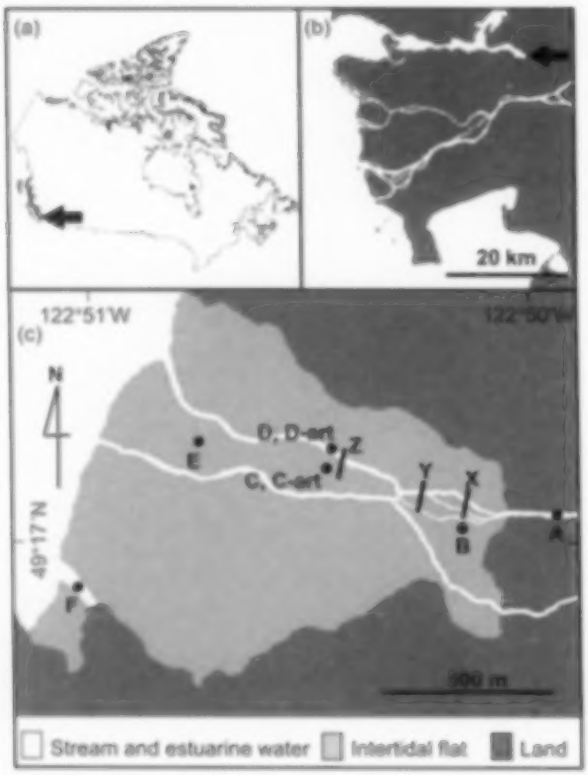
Fig. 1. The intertidal flat studied in the Nooms Creek estuary near Vancouver, British Columbia, Canada (49°17′N, 122°50′W). Bars and solid circles in the map indicate transects for sampling deposited leaves (X–Z) and stations for the leaf pack experiment (stations A–F), respectively. Stations C-art and D-art indicate the places where artificial leaf packs were placed beside stations C and D, respectively.



packs, air-dried, senescent alder leaves weighing 5.0 g (to the nearest 0.05 g) were put into nylon bags with 10 mm mesh. For artificial leaf packs, polyester cloth cut into a size and shape similar to that of natural alder leaves was put into a different set of nylon bags. On 1 September 2004, the leaf packs were placed on sediment surfaces in the field and tied to nylon ropes anchored by bricks. The leaf packs were sampled 2, 9, 21, 35, 52, and 105 days later after their initial submersion. The air and stream water temperatures for September to December 2004 ranged from 1.7 to 18.4 °C (daily means) and from 7.0 to 13.5 °C (five measurements), respectively. The seawater temperature for September to October 2004 at station F ranged from 12.5 to 16.5 °C (three measurements).

After sampling the leaf packs, leaves were taken out of the nylon bags and washed well with <500 mL tap water on a 0.5 mm sieve in the laboratory. The water that passed through the sieve was kept to measure the amount of fine material accumulated on leaves. All of the visible leaf debris and invertebrates on the sieve were picked out using tweezers. The leaf samples were dried at 60 °C for 48 h, and their organic matter amount was determined by dry mass loss on combustion at 550 °C for 2 h. For the samples of day 52 at stations A, C, and F, leaf subsamples (ca. 0.3 g) were taken for carbon and nitrogen analysis. The mass of the subsample of each leaf pack was later added back to its organic matter amount for leaf organic matter amount determination based on the relationship between leaf dry mass and organic matter content (loss on combustion). The invertebrates collected from the leaf packs were preserved in 70% ethanol, identified, and counted. For the day 52 samples of both natural and artificial leaf packs at stations C and C-art, 10 to 15 individuals of *Monocorophium insidiosum* (amphipod), which numerically predominated our invertebrate samples, were preserved at –20 °C for later carbon and nitrogen stable isotope analyses. To determine the initial conditions of the leaves that were used for the leaf pack experiment, air-dried alder leaves were also preserved in a –20 °C freezer at the beginning of the experiment and later analysed for organic content, carbon, and nitrogen.

The amount of fine particulate matter (including inorganic and organic) (FPM) and fine particulate organic matter (FPOM) on the leaves was also quantified for all the leaf pack samples. Because fine particulate materials on the leaves were composed of uneasily depositing fine fractions and easily depositing coarse fractions, the amounts of these fractions were determined in different ways and combined. For the fine fractions, the water that was used for washing the leaf samples was adjusted to 500 mL in a bottle and well shaken. Then the turbid upper layer water of about 30–50 mL was collected swiftly, measured to an accurate volume, and filtered through precombusted, preweighed glass fibre filters (AE/E). These filters were dried at 60 °C for 48 h and then combusted at 550 °C for 2 h. For the coarse fractions, the slurry deposited on the bottom of the above-mentioned bottles was put on aluminum dishes, dried at 60 °C for 48 h, and combusted at 550 °C for 2 h. Then the total amount (in mg) of FPM and FPOM on leaves were determined by the following equations:

$$(1) \qquad \mathrm{FPM} = \mathrm{FPM}_f \cdot \frac{W}{w} + \mathrm{FPM}_d$$

$$(2) \qquad \mathrm{FPOM} = \mathrm{FPOM}_f \cdot \frac{W}{w} + \mathrm{FPOM}_d$$

where FPM_f and FPM_d represent dry mass (in mg) of samples on the filters and dishes, respectively, FPOM_f and FPOM_d represent dry mass loss (in mg) on combustion for the filter and dish samples, respectively, w is volume of filtered water (mL), and W is water volume that was used for washing leaves (500 mL).

Carbon and nitrogen analysis

The frozen leaf and amphipod samples were dried at 60 °C for 48 h immediately before processing. The samples were ground by mortar and pestle and then analysed for carbon and nitrogen content and carbon and nitrogen stable isotopes. These samples were analysed by a continuous flow isotope ratio mass spectrometer system (Europa Hydra 20/20) at the University of California Davis Stable Isotope Facility (Davis, California). Isotopic compositions were reported as parts per thousand deviations (‰) from Pee Dee Belemnite for carbon ($\delta^{13}C$) and from air for nitrogen ($\delta^{15}N$).

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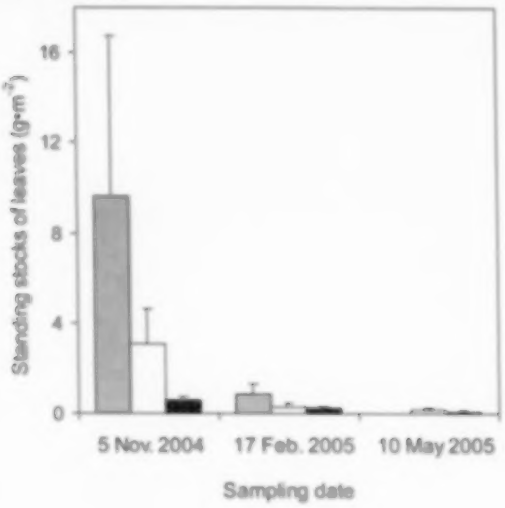
Fig. 2. Seasonal and spatial variation in standing stocks of leaves on the transects (mean ± standard error, $n = 3$). Shaded bars, transect X; open bars, transect Y; solid bars, transect Z.



Data analyses

Both leaves deposited on the tidal flat sediment and remnant leaves in the leaf packs showed simple decreasing trends in the amount of material, so they were fit to the exponential model:

$$(3) \qquad M_t = M_0 \cdot e^{-kt}$$

where M_t is leaf dry mass (determined as loss on combustion) at time t, M_0 is initial leaf dry mass, and k is leaf decrease rate coefficient. The k for deposited leaves (k_1) indicates subsequent net decrease rate resulting from physical import and export of leaves and leaf breakdown. On the other hand, the k for leaf packs (k_2) shows leaf breakdown rate. To test whether k_2 differed significantly between the stations, analysis of covariance (ANCOVA) was conducted; the interaction terms of station (factor) and time (covariate) were analysed.

Nonparametric, multiple comparisons by the Steel–Dwass test were conducted to examine whether the numbers of invertebrates and species in leaf packs differed between the stations and whether leaf type (natural vs. artificial) affected invertebrate colonisation. To explore factors governing invertebrate colonisation in leaf packs, linear regression analyses were conducted for relationships of invertebrate numbers with days after the leaf pack submersion and with FPM and leaf amounts, dividing the period of the leaf pack experiment into before day 21 and after day 21. Furthermore, the difference in C:N between the leaf samples was tested by ANOVA, followed by Tukey's honestly significant difference (HSD) test. Multiple analyses of variance (MANOVA) were conducted to test differences in the stable isotope signatures between the amphipods and between the leaf samples. The MANOVA was followed by calculation of least square means for multiple comparisons.

Table 1. Rate coefficients (exponents of the negative exponential model) for decrease in standing stock of leaves on the transects (k_1) and leaf breakdown in the leaf packs (k_2).

Transects or stations[a]	k_1 or k_2[a]	SE	r^2	p	n
Deposited leaves					
X	0.0391	0.0078	0.78	0.0016	9
Y	0.0227	0.0080	0.53	0.0252	9
Z	0.0228	0.0077	0.55	0.0217	9
Leaf pack					
A	0.0079	0.0019	0.57	0.0011	15
B	0.0057	0.0009	0.72	<0.0001	17
C	0.0064	0.0009	0.77	<0.0001	18
D	0.0085	0.0007	0.91	<0.0001	18
E	0.0265	0.0038	0.76	<0.0001	18
F	0.0133	0.0028	0.69	0.0008	12

Note: SE, standard error; r^2, coefficient of determination; p, probability; n, sample number.
[a]Transects and k_1 for deposited leaves; stations and k_2 for leaf pack.

SAS version 9.1 (SAS Institute Inc., Cary, North Carolina) was used for all the statistical analyses in the present study. For the Steel–Dwass test, we used a SAS program developed by Hamada and Yamamoto (1999) applying the PROBMC function.

Results

Standing stock of leaves

The mean values of standing stocks of deciduous leaves in the tidal flat decreased with distance from the stream mouth (Fig. 2). They also decreased with time during the sampling term, high in fall and low in spring. The highest standing stock was observed at 23.8 g·m^{-2} on transect X in November 2004. Leaves were deposited on all the sampling plots in November 2004 and February 2005, whereas they were not observed at four sampling plots in May 2005. The rate coefficient for temporal decrease in standing stock of leaves, k_1, was the highest on transect X and almost equivalent between transects Y and Z (Table 1).

Leaf breakdown and invertebrate colonisation in leaf packs

At station F, leaf packs were not collected for days 9 and 105 because of missing samples. The leaf mass in the leaf packs decreased consistently with time in all the stations. The leaf breakdown rate in the leaf packs, k_2, differed significantly between the stations (ANCOVA, $F_{5,85} = 17.61$, $p < 0.0001$) (Table 1). The k_2 was lower at the stations in the upper intertidal parts of the tidal flat and the stream channel, i.e., stations A, B, C, and D, than at the stations in the lower intertidal and subtidal parts, i.e., stations E and F. The highest k_2, 0.0265·day^{-1} in station E, is almost five times as large as the lowest one, 0.0057·day^{-1} in station B. In the upper intertidal parts (transect X–Z and stations B and C), k_2 was smaller than k_1 (factor of about 4–6.5).

The total numbers of invertebrates and species in the leaf packs did not differ significantly between the stations (Fig. 3). We observed 12 species in this study, of which Amphipoda numerically dominated at all the stations;

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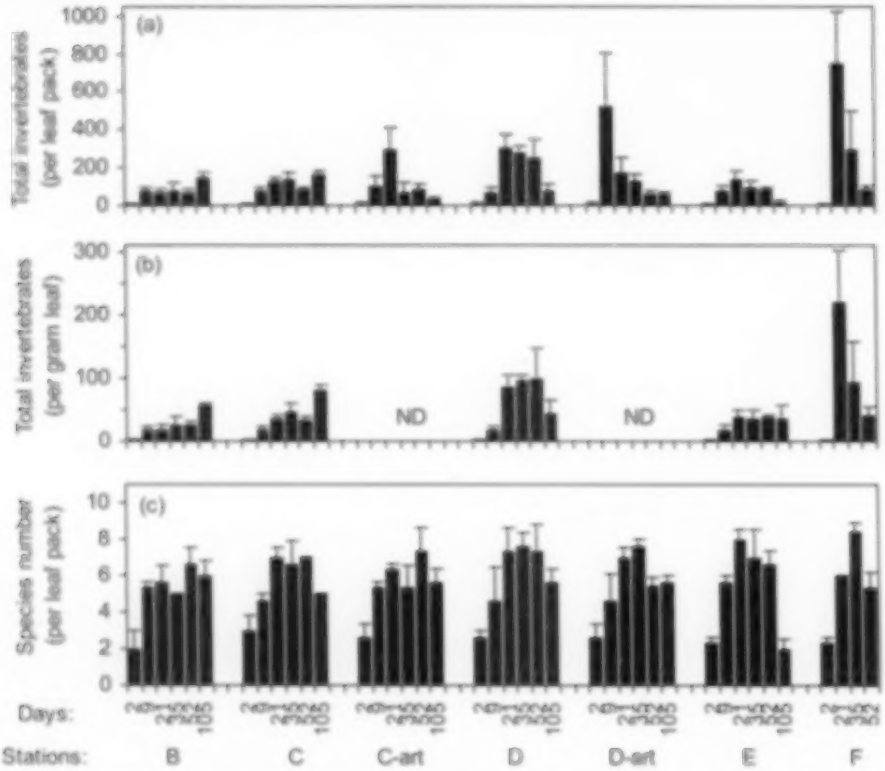
Fig. 3. The numbers (mean ± standard error, $n = 3$) of total macroinvertebrates (*a*) per leaf pack and (*b*) per gram of leaf and (*c*) the numbers of species colonising leaf packs. The Steel–Dwass test did not detect a significant difference between the stations ($p > 0.05$ for all combinations of the stations). Note the different *y* axis scales between panels.



M. insidiosum was the most numerous, followed by *Locustogammarus levingsi* and *Ampithoe valida* (Fig. 4). The number of *M. insidiosum* and *Hemigrapsus oregonensis* (Decapoda, crab) were not significantly different between the stations. *Locustogammarus levingsi* (Amphipoda) abundance was relatively low at station C-art and high at stations D, D-art, and E. *Zeuxo normani* (Tanaidacea) was relatively low at station F and high at station C. *Haliplanella* sp. (Actiniaria, anemone) and Polychaeta were relatively abundant at stations C and F, respectively. No species showed significant differences in their numbers between natural and artificial leaf packs.

In the leaf pack experiment, the maximum densities of most invertebrate species were observed between days 21 and 52. Until day 21, the amount of accumulated FPM, the number of invertebrates, and species number increased with time (Fig. 4; Table 2). After day 21, temporal trends differed between species (Fig. 4). *Monoporeiphium insidiosum* tended to decrease significantly along with the decrease in leaf amount after day 21 (Table 2). Both *Z. normani* and *H. oregonensis* differed in temporal, numerical trends between stations but showed tight relationships with FPM amount rather than amount of remaining leaves after day 21 (Table 2). FPM and FPOM were significantly correlated both before and after day 21 (before day 21, $r = 0.99$, $p < 0.0001$; after day 21, $r = 0.60$, $p = 0.014$).

Chemical properties of leaves and amphipods

Leaves incubated in stations A, C, and F showed significant decreases in C:N by day 52 compared with the ratio at the beginning of the incubation (ANOVA, $F_{[3,8]} = 23.11$, $p = 0.0003$) (Fig. 5). For the day 52 samples, the mean value of leaf C:N was the lowest at station F and the highest at station A, although no statistically significant differences were detected between the stations. MANOVA showed that leaf $\delta^{13}C$ and $\delta^{15}N$ were enhanced during the 52-day incubation (Wilks' Lambda, $F_{[6,14]} = 7.15$, $p = 0.001$) (Fig. 6). Leaf $\delta^{13}C$ was enhanced significantly only in station F (least square means, $p = 0.008$). Leaf $\delta^{15}N$ was enhanced significantly in all of stations A, C, and F, and leaf $\delta^{15}N$ in day 52 was more enhanced in stations C and F than station A (least square means, $p \leq 0.019$). The amphipods from both natural and artificial leaf packs and ambient amphipods showed no significant differences in their isotope signatures (MANOVA, Wilks' Lambda, $F_{[4,10]} = 3.32$, $p = 0.056$). Both $\delta^{13}C$ and $\delta^{15}N$ of amphipods deviated from the signatures of leaves but were close to those of benthic microalgae.

Discussion

Leaf retention and breakdown in the estuarine tidal flat

Based on our measurements on the transects along with visual observations, areas of leaf deposit appeared to be lim-

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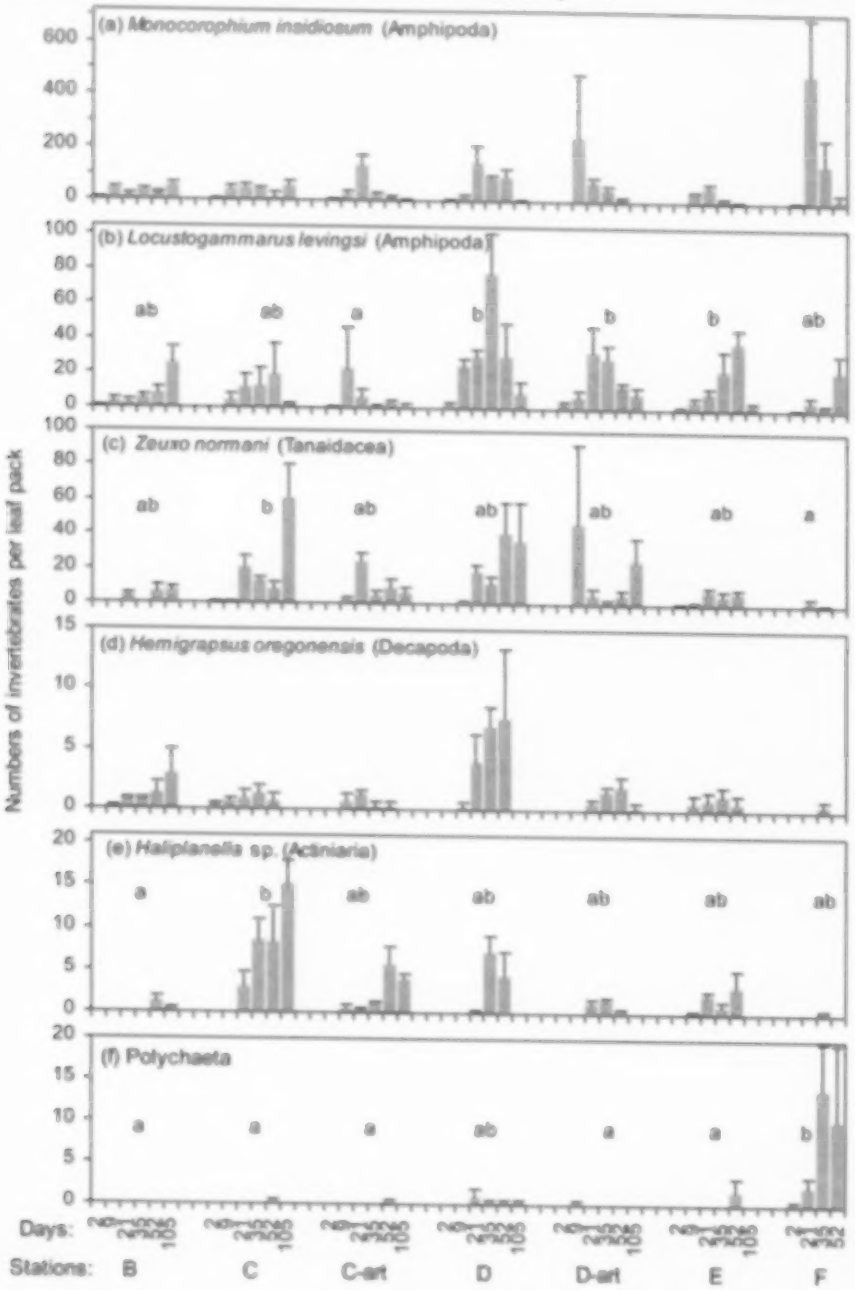
Fig. 4. The numbers (mean ± standard error, $n = 3$) of invertebrates (per leaf pack) colonising leaf packs: (*a*) *Monocorophium insidiosum* (Amphipoda), (*b*) *Locustogammarus levingsi* (Amphipoda), (*c*) *Zeuxo normani* (Tanaidacea), (*d*) *Haliplanella* sp. (Actiniaria, anemone), (*e*) *Hemigrapsus oregonensis* (Decapoda, crab), and (*f*) Polychaeta. Different letters indicate significant differences between the stations (Steel–Dwass test, $p < 0.05$). Note the different *y* axis scales between panels.


(a) Monocorophium insidiosum (Amphipoda)
(b) Locustogammarus levingsi (Amphipoda)
(c) Zeuxo normani (Tanaidacea)
(d) Hemigrapsus oregonensis (Decapoda)
(e) Haliplanella sp. (Actiniaria)
(f) Polychaeta
Numbers of invertebrates per leaf pack
Days:
Stations: B C C-art D D-art E F

ited to near the stream mouth and along the stream channel of the upper part of the tidal flat. In this part, the observed standing stock of leaves, <23.8 g·m^{-2}, was of the same order of magnitude as that in streams (Richardson 1992*b*; Delong and Brusven 1993; González and Pozo 1996). The standing stocks had a seasonal trend: leaves were deposited in fall and most of them disappeared by spring. This trend is quite similar to one of deciduous tree leaves in some headwater streams (Richardson 1992*b*), and the timing of leaf litter input to the stream was probably a significant predictor for the

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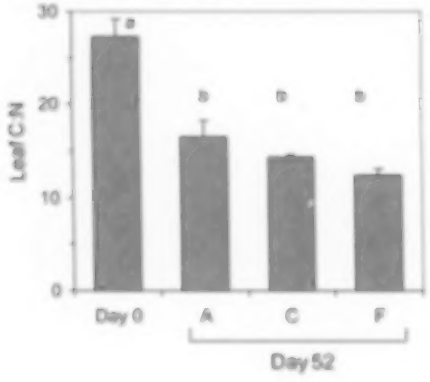
Table 2. Results of linear regression analyses for day since leaf pack submersion, amount of remaining leaves, amount of fine particulate matter (FPM) accumulated in leaf packs, and invertebrate numbers in leaf packs.

	Independent					
	Before day 21			After day 21		
Dependent	Day	Leaf	FPM	Day	Leaf	FPM
Leaf	0.40**, –	—	0.08, –	0.55***, –	—	0.00, +
FPM	0.19*, +	0.08, –	—	0.07, +	0.00, +	—
Monocorophium insidiosum	0.25*, +	0.24, –	0.03, +	0.14, –	0.32*, +	0.35, +
Lewistogammarus levingsi	0.26*, +	0.05, –	0.30*, +	0.10, –	0.06, +	0.06, +
Ampithoe valida	0.40**, +	0.42*, –	0.05, +	0.30*, –	0.18, +	0.01, +
Zeuxo normani	0.17, +	0.36*, –	0.10, +	0.19*, +	0.01, –	0.76***, +
Haliplanella sp.	0.34**, +	0.18, –	0.00, +	0.00, +	0.03, +	0.01, +
Hemigrapsus oregonensis	0.35**, +	0.17, –	0.88***, +	0.08, –	0.13, +	0.64**, +
Polychaetes	0.12, +	0.26, –	0.08, +	0.06, –	0.02, +	0.07, –
Total individual number	0.31*, +	0.29*, –	0.06, +	0.12, –	0.34*, +	0.14, +
Species number	0.86***, +	0.24, –	0.22*, +	0.32, –	0.69, +	0.01, +

Note: The experiment period was divided into two phases: days 2–21 (before day 21) and days 35–105 (after day 21). The results are shown as coefficients of determination (significance: *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$). Plus and minus signs indicate positive and negative relationships, respectively.

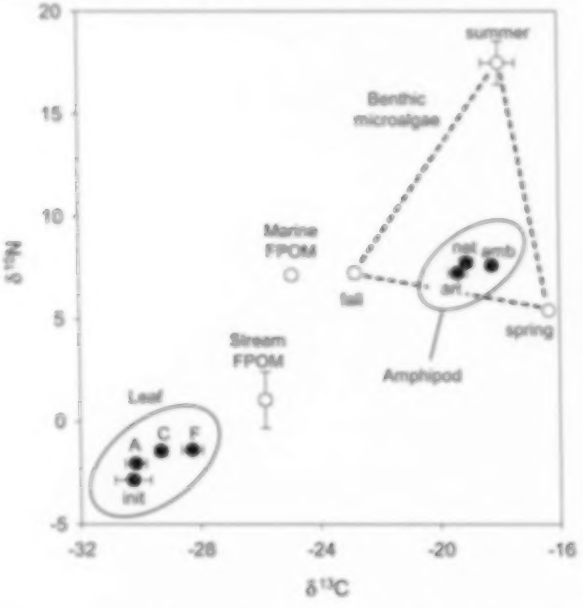
Fig. 5. Carbon–nitrogen mass ratio (mean ± standard error, $n = 3$) of leaves in leaf packs for day 0 (initial condition) and day 52 at stations A, C, and F. Different letters indicate significant differences between the stations (Tukey's honestly significant difference (HSD) test, $p < 0.05$).



temporal trend in the standing stock of leaves in the tidal flat. In addition, the fact that k_2 was significantly smaller than k_1 indicates that leaf breakdown due to biological processes did not significantly contribute to the observed decreases in standing stock, and physical export may have been the dominant process in the decreases.

The alder leaf breakdown rates in our leaf pack experiment (k_2), 0.0057–0.0265·day^{-1}, were within the range, 0.004–0.047·day^{-1}, determined in headwater streams of the same region under a wide range of temperatures, 2.0–13.4 °C (Richardson 1992*b*). Hoover et al. (2006) experimentally demonstrated that breakdown of alder leaves was slower in riffle stations with relatively high sheer stresses and suggested that the leaf breakdown was accounted for by biological processes rather than mechanical fragmentation. Our results also showed that leaf breakdown was relatively slower in the stations within the stream channel, i.e., stations A and C, although the shear stresses were expected to be relatively stronger due to the stream current. Thus, the spatial variation in breakdown rates of the leaf packs in this study was probably not attributable to mechanical fragmentation differing among the stations.

Fig. 6. $\delta^{13}C$ and $\delta^{15}N$ (mean ± standard error, $n = 3$) of leaves and amphipods (*Monocorophium insidiosum*) in leaf packs. For leaves: init, initial leaves before submersion (day 0); A, C, and F, stations A, C, and F (day 52). For amphipods: amb, ambient amphipods; nat, amphipods from natural leaves in station C (day 52); art, amphipods from artificial leaves in station C (day 52). $\delta^{13}C$ and $\delta^{15}N$ of marine fine particulate organic matter (FPOM) ($n = 4$), stream FPOM ($n = 12$), benthic microalgae ($n = 3$ for each season), and ambient amphipods ($n = 3$, July 2004) are cited from research conducted in the same tidal flat in 2004–2005 (T. Sakamaki and J.S. Richardson, unpublished data).



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Many studies in freshwater have shown a significant contribution of macroinvertebrates to leaf breakdown (e.g., Richardson 1992*a*; Wallace et al. 1997; Hieber and Gessner 2002). In our leaf pack experiment, however, k_2 differed significantly between the stations, despite no significant difference in total number of invertebrates occupying the leaf packs. Particularly in station E, although it was distinct that the invertebrate number was not higher than those of the other stations, k_2 was the highest. These facts suggest that leaf breakdown in the tidal flat was attributable not to invertebrates but to microbial processes. In a tidally affected freshwater system, Hill and Perrote (1995) also reported a case of significant contributions of microbial activities to breakdown of terrestrial leaves. In addition, previous studies in estuaries showed that bacteria on terrestrial plant detritus with relatively low nitrogen content incorporated nitrogen from ambient water resulting in C:N increase and $\delta^{15}N$ enhancement (Findlay and Tenore 1982; Caraco et al. 1998). Thus, the decrease in C:N and enhancement of $\delta^{15}N$ in our leaf pack experiment were also probably attributable to bacterial activity.

Richardson (1992*b*) demonstrated strong positive relationships between alder leaf breakdown rate and temperature. Air temperature was lower than water temperature at times during our leaf pack experiment, which was conducted in fall to early winter. Longer periods of submersion in the relatively warmer seawater and supporting higher microbial activities are a probable explanation for the higher leaf breakdown rate (k_2) in the lower intertidal and subtidal areas, i.e., stations E and F.

Leaf utilisation by tidal flat invertebrates

Until day 21 of the leaf pack experiment, time was the most important factor for invertebrate colonisation. The observed times for most invertebrate species to reach their maximum numbers, 21–52 days, were equivalent with times for invertebrate colonisation in streams (e.g., Richardson 1992*a*; Hieber and Gessner 2002). After day 21, the factors governing invertebrate colonisation likely differed between species, e.g., the number of *M. insidiosum* likely depended on the amount of remaining leaves, whereas the numbers of *Z. normani* and *H. oregonensis* were significantly related to FPM amount accumulated on leaves. Specific factors governing colonisation of the other species, e.g., *L. levingsi*, *Haliplanella* sp., and polychaetes, were not found, as they did not show significant relationships with the variables tested.

The result that invertebrate densities did not significantly differ between natural and artificial leaf packs indicates the contribution of leaves mainly as habitat rather than food source. In addition, the fact that the stable isotope signatures of *M. insidiosum* did not significantly differ between ambient habitat, artificial, or natural leaf packs also supports their use of leaves as habitat. An experiment by Kochi and Yanai (2006) also suggested that estuarine amphipods used oak leaves mainly as habitat, consistent with our results. Richardson (1992*a*) showed that in streams, colonisation of leaf packs by some nonshredders was associated with FPOM accumulation, suggesting their use of FPOM as food source. However, in contrast to streams that retain less FPOM, the tidal flat has abundant ambient FPOM. Hence, in the tidal flat, the FPM-associated colonisation of the leaf packs by the invertebrates, i.e., *Z. normani* and *H. oregonensis*, probably did not aim for FPOM as a food source. The complex of FPM and leaves may have provided habitat suitable for them.

In tidal flats, benthic microalgae is highly productive and reported to be the dominant food source for benthic invertebrates (e.g., Kang et al. 2003; Yokoyama and Ishihi 2003). Our results for amphipod $\delta^{13}C$ and $\delta^{15}N$ also indicated that the amphipods assimilated a substantial proportion of their diet from benthic microalgae in our study site. In general, algal material is thought to have higher nutritional value than terrestrial organic material because of its relatively low C:N. This may have led to the contribution of the leaves not as food source, but as habitat in the tidal flat, whereas there are invertebrates that shred leaves and feed directly on them in streams, i.e., shredders (e.g., Richardson 1991, 1992*a*; Wallace et al. 1997).

Our study demonstrated that leaves were not directly assimilated by invertebrates and likely primarily provided microhabitats in the tidal flat. However, leaves can be finely fragmented and nutritionally enhanced through microbial mediation (Findlay and Tenore 1982; Caraco et al. 1998). Effects of such processes on estuarine invertebrates need to be examined in further studies in order to conclude on the role of terrestrial leaf material in estuaries. Furthermore, amphipods, the most significant users of leaves in our study, are thought to be an important food source for fish in estuarine ecosystems (e.g., Levings et al. 2004; Hampel et al. 2005). Hence, further studies may also need to evaluate the temporary but substantial provision of invertebrate microhabitats by terrestrial leaf inputs in terms of contribution to higher trophic level consumers.

Acknowledgements

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References

Canhoto, C., and Graça, M.A.S. 1996. Decomposition of *Eucalyptus globulus* leaves and three native leaf species (*Alnus glutinosa*, *Castanea sativa* and *Quercus faginea*) in a Portuguese low order stream. Hydrobiologia, **333**: 79–85.

Caraco, N.F., Lampman, G., Cole, J.J., Limburg, K.E., Pace, M.L., and Fischer, D. 1998. Microbial assimilation of DIN in a nitrogen rich estuary: implications for food quality and isotope studies. Mar. Ecol. Prog. Ser. **167**: 59–71.

Chanton, J., and Lewis, F.G. 2002. Examination of coupling between primary and secondary production in a river-dominated estuary: Apalachicola Bay, Florida, U.S.A. Limnol. Oceanogr. **47**: 683–697.

Delong, M.D., and Brusven, M.A. 1993. Storage and decomposition of particulate organic matter along the longitudinal gradient of an agriculturally-impacted stream. Hydrobiologia, **262**: 77–88.

Dudgeon, D., and Wu, K.K.Y. 1999. Leaf litter in a tropical stream: food or substrate for macroinvertebrates? Arch. Hydrobiol. **146**: 65–82.

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Findlay, S., and Tenore, K. 1982. Nitrogen source for a detritivore: detritus substrate versus associated microbes. Science (Washington, D.C.), **218**: 371–373.

González, E., and Pozo, J. 1996. Longitudinal and temporal patterns of benthic course particulate organic matter in the Agüera stream (northern Spain). Aquat. Sci. **58**: 355–366.

González, J.M., and Graça, M.A.S. 2003. Conversion of leaf litter to secondary production by a shredding caddisfly. Freshw. Biol. **48**: 1578–1592.

Hamada, C., and Yamamoto, N. 1999. Separate-ranking nonparametric multiple comparison. *In* Proceeding of 18th SAS User Group International, 23 August 1999, Tokyo, Japan. pp. 383–390. (In Japanese.) SAS Institute Japan, Tokyo.

Hampel, H., Cattrijse, A., and Elliott, M. 2005. Feeding habits of young predatory fishes in marsh creeks situated along the salinity gradient of the Schelde estuary, Belgium and the Netherlands. Helgol. Mar. Res. **59**: 151–162.

Hein, T., Baranyi, C., Herndl, G.J., Wanek, W., and Schiemer, F. 2003. Allochthonous particulate organic matter in floodplains of the River Danube: the importance of hydrological connectivity. Freshw. Biol. **48**: 220–232.

Hieber, M., and Gessner, M.O. 2002. Contribution of stream detritivores, fungi, and bacteria to leaf breakdown based on biomass estimates. Ecology, **83**: 1026–1038.

Hill, B.H., and Perrotte, W.T., Jr. 1995. Microbial colonization, respiration, and breakdown of maple leaves along a stream–marsh continuum. Hydrobiologia, **312**: 11–16.

Hoover, T.M., Richardson, J.S., and Yonemitsu, N. 2006. Flow–substrate interactions create and mediate leaf litter resource patches in streams. Freshw. Biol. **51**: 435–447.

Johnson, S.L., and Covich, A.P. 1997. Scales of observation of riparian forests and distributions of suspended detritus in a prairie river. Freshw. Biol. **37**: 163–175.

Kang, C.K., Kim, J.B., Lee, K.S., Kim, J.B., Lee, P.Y., and Hong, J.S. 2003. Trophic importance of benthic microalgae to macrozoobenthos in coastal bay systems in Korea: dual stable C and N isotope analysis. Mar. Ecol. Prog. Ser. **259**: 79–92.

Kasai, A., and Nakata, A. 2005. Utilization of terrestrial organic matter by the bivalve *Corbicula japonica* estimated from stable isotope analysis. Fish. Sci. **71**: 151–158.

Kochi, K., and Yanai, S. 2006. Decomposition of leaves in coastal brackish water and their use by the macroinvertebrate *Anisogammarus pugettensis* (Gammaridea). Mar. Freshw. Res. **57**: 545–551.

Kuwae, T., Kibe, E., and Nakamura, Y. 2003. Effect of emersion and immersion on the porewater nutrient dynamics of an intertidal sandflat in Tokyo Bay. Estuar. Coast. Shelf Sci. **57**: 929–940.

Levings, C.D., Barry, K.L., Grout, J.A., Piercey, G.E., Marsden, A.D., Coombs, A.P., and Mossop, B. 2004. Effects of acid mine drainage on the estuarine food web, Britannia Beach, Howe Sound, British Columbia, Canada. Hydrobiologia, **525**: 185–202.

Motomori, K., Mitsuhashi, H., and Nakano, S. 2001. Influence of leaf litter quality on the colonization and consumption of stream invertebrate shredders. Ecol. Res. **16**: 173–192.

Munson, S.A., and Carey, A.E. 2004. Organic matter sources and transport in an agriculturally dominated temperate watershed. Appl. Geochem. **19**: 1111–1121.

O'Brien, D.J., Whitehouse, R.S.J., and Cramp, A. 2000. The cyclic development of a macrotidal mudflat on varying timescales. Contin. Shelf Res. **20**: 1593–1619.

Richardson, J.S. 1991. Seasonal food limitation of detritivores in a montane stream: an experimental test. Ecology, **72**: 873–887.

Richardson, J.S. 1992*a*. Food, microhabitat, or both? Macroinvertebrate use of leaf accumulations in a montane stream. Freshw. Biol. **27**: 169–176.

Richardson, J.S. 1992*b*. Course particulate detritus dynamics in small, montane streams of southwestern British Columbia. Can. J. Fish. Aquat. Sci. **49**: 337–346.

Richardson, J.S., Shaughnessy, C.R., and Harrison, P.G. 2004. Litter breakdown and invertebrate association with three types of leaves in a temperate rainforest stream. Arch. Hydrobiol. **159**: 309–325.

Robinson, C.T., and Gessner, M.O. 2000. Nutrient addition accelerates leaf breakdown in an alpine springbrook. Oecologia, **122**: 258–263.

Sakamaki, T., Nishimura, O., and Sudo, R. 2006. Tidal time-scale variation in nutrient flux across the sediment–water interface of an estuarine tidal flat. Estuar. Coast. Shelf Sci. **67**: 653–663.

Sponseller, R.A., and Benfield, E.F. 2001. Influence of land use on leaf breakdown in southern Appalachian headwater streams: a multiple-scale analysis. J. North Am. Benthol. Soc. **20**: 44–59.

Thornton, S.F., and McManus, J. 1994. Application of organic carbon and nitrogen stable isotope and C/N ration as source indicator of organic matter provenance in estuarine systems: evidence from the Tay Estuary, Scotland. Estuar. Coast. Shelf Sci. **38**: 219–233.

Uncles, R.J., and Stephens, J.A. 2000. Observations of currents, salinity, turbidity and intertidal mudflat characterestics and properties in the Tavy Estuary, UK. Contin. Shelf Res. **20**: 1531–1549.

Wallace, J.B., Eggert, S.L., Meyer, J.L., and Webster, J.R. 1997. Multiple trophic levels of a forest stream linked to terrestrial litter inputs. Science (Washington, D.C.), **277**: 102–104.

Wipfli, M.S., Richardson, J.S., and Naiman, R.J. 2007. Ecological linkages between headwaters and downstream ecosystems: transport of organic matter, invertebrates, and wood down headwater channels. J. Am. Water Resour. Assoc. **43**: 1–14.

Yokoyama, H., and Ishihi, Y. 2003. Feeding of the bivalve *Theora lubrica* on benthic microalgae: isotopic evidence. Mar. Ecol. Prog. Ser. **255**: 303–309.

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Phytoplankton species turnover controlled by physical forcing at different time scales

Alexandrine Pannard, Myriam Bormans, and Yvan Lagadeuc

Abstract: Changes in the physical and chemical environment induced by forcing events such as wind and rain can control the short-term dynamics of the phytoplankton community of inland waters. In two temperate reservoirs, species composition, diversity index, and species dynamics were characterized over periods of 3 weeks during different seasons, in parallel with changes in the physical and chemical structure of the water column. Dominant species and diversity index were shown to be controlled by environmental factors fluctuating on a seasonal and weekly time scale, whereas some rarer species responded to wind events and were indicators of a very short-term environmental change. As a consequence of the response of indicator species, the rate of change in species composition increased following meteorological events. Shifts in species composition were observed during each sampling period, except during the strongest stratification period. The shifts were associated with a modification of resource availability or intensity of stratification. We found that the resistance of the phytoplankton community to short-term physical forcing by wind increased with intensity of stratification. After the forcing event, the community did not return to its original structure because of modifications of the physical and chemical conditions induced by meteorological forcing on a weekly time scale.

Résumé : Cette étude met en évidence la dynamique à court terme des communautés de phytoplancton lacustre en réponse aux modifications de l'environnement physico-chimique induites par des événements de forçage, comme le vent et la pluie. Dans deux réservoirs tempérés, l'indice de diversité, la dynamique des espèces et la composition en espèces ont été suivis sur des périodes de 3 semaines à différentes saisons, en parallèle avec les modifications de la structure physico-chimique de la colonne d'eau. Les espèces dominantes et l'indice de diversité étaient contrôlés à des échelles de temps saisonnière et hebdomadaire, alors que certaines espèces plus rares indicatrices de changements à très court terme ont répondu aux événements de vent. En conséquence de la réaction des espèces indicatrices le taux de changement des espèces a augmenté après les événements rapides de forçage. Des modifications brutales de la composition en espèces ont été observées pendant chaque campagne d'échantillonnage, excepté pendant la période de stratification maximale. Ces changements étaient associés à des modifications de la disponibilité des ressources ou de l'intensité de la stratification. Nous avons observé que la résistance de la communauté de phytoplancton au forçage physique à court terme par le vent augmentait avec l'intensité de la stratification. Après les événements de forçage, la communauté n'est pas retournée à sa structure initiale, à cause de modifications entre-temps des conditions physico-chimiques, induites par le forçage météorologique sur une échelle de temps hebdomadaire.

Introduction

The periodicity of phytoplankton community composition in lakes as a result of seasonal variations in physical forcing has often been investigated (Lewis 1978*b*; Noges et al. 1998; Anneville et al. 2002). Seasonal physical forcing is mainly due to factors such as changes in air temperature and solar radiation (Sommer et al. 1986), which control the vertical structure of the water column of a lake, water temperature, depth of the mixed layer, intensity of mixing, and consequently the nutrients available in the surface layer. The vertical structure of the water column can also be modified on a shorter time scale by forcing events such as wind and rain (Imberger and Parker 1985; MacIntyre et al. 1999). These modifications take place on a time scale of a few days, similar to the time scale of the phytoplankton doubling, and can thus influence the phytoplankton community (Reynolds 1984*b*). Modification of the vertical structure of the water column on different time scales, from seasonal to daily, may thus affect the dynamics of the phytoplankton community. Three time scales are used here, short term (a few days), intermediate (the sampling period of 3 weeks), and seasonal,

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with a focus on the short term, as very few studies have examined the dynamics of phytoplankton at that time scale.

The vertical structure of the water column is a determining factor for the phytoplankton community, as it controls both losses by sedimentation rate and growth through nutrient and light availability. Meteorological forcing events can modify this vertical structure in several ways. For example, the mixed-layer depth can be increased, leading to lower light availability over the mixed layer (Diehl et al. 2002) and a decrease in sedimentation losses (Ptacnick et al. 2003), as well as an increase in the intensity of mixing and redistributing phytoplankton populations over depth. Species able to regulate their buoyancy, which therefore become concentrated during calm periods (Klausmeier and Litchman 2001), may be disadvantaged by this redistribution, as they temporarily lose their vertical position (Huisman et al. 2004). Species that tend to sink will be mixed through the water column and their sedimentation loss rate will thus be reduced (Huisman et al. 2002). Lastly, forcing events can modify nutrient availability by breaking down or weakening the nutricline or by modifying external inputs from the drainage basin. The resulting change in competition between species with different nutrient requirements and storage capacity may affect phytoplankton community structure (Sommer 1985); therefore meteorological forcing events may induce a short-term variability in the phytoplankton community.

In a previous study, we showed that short-term forcing events can modify both the size structure of phytoplankton and losses via sedimentation (Pannard et al. 2007). In this study, we address physical and chemical forcing at different time scales, with a focus on time scales of a few days. We use diversity index, rate of change of species composition and species community structure, to examine short-term dynamics of phytoplankton community during different seasons in two temperate reservoirs.

Materials and methods

Study sites

Two stratified temperate reservoirs located in Brittany, near Rennes (France), were studied (Fig. 1). La Cheze and Rophemel are both drowned river reservoirs. The volume of La Cheze is about 15×10^6 m^3, with a mean depth of 14 m, whereas the smaller Rophemel reservoir has a volume of 5×10^6 m^3 and a mean depth of about 6.5 m (Table 1). The reservoirs differ in their exposure to wind in terms of fetch (Table 1) and orientation to the dominant wind direction (Fig. 1), with La Cheze being more exposed to wind forcing than Rophemel. The reservoir of La Cheze has a smaller catchment area of about 30 km^2, with a lake surface area of about 1 km^2 and a residence time between 3 months and 1 year, whereas Rophemel has a large catchment area (380 km^2) with a residence time between 1 and 4 weeks (Table 1).

Sampling

The reservoir of La Cheze was sampled during three seasons, summer (20 June 2003 – 14 July 2003), autumn (22 September 2003 – 14 October 2003), and early spring (24 March 2004 – 15 April 2004). Rophemel was sampled only in spring (5 May 2004 – 24 May 2004). For each period, sampling was performed in the morning (0900 h), every 2 or 3 days, a few hundred metres from the outlet of the reservoir and in the vicinity of the old river bed, far away from tributaries. Water samples were collected using a 1 m integrated vertical sampler (single-valve bailer) at four depths (1, 7, 13, and 21 m for La Cheze and 1, 5, 9, and 14 m for Rophemel) and analysed for nutrient and phytoplankton species community structure.

Physical and chemical structure

To characterize the physical forcing, meteorological data monitored in Rennes by Meteo France were used (Fig. 1). Wind speed and direction (collected 10 m above the ground), solar radiation, and mean air temperature were averaged daily, whereas rainfall was measured daily.

To determine the water column stratification intensity, the potential energy (PE), which represents the quantity of energy needed to homogenize the entire water column (Lagadeuc et al. 1997), was calculated (in J·m^{-3}) using the formula

$$\text{PE} = \frac{1}{h}\int_0^h (\bar{\rho} - \rho) g z \, \mathrm{d}z \quad (1)$$

based on the mean density

$$\bar{\rho} = \frac{1}{h}\int_0^h \rho \, \mathrm{d}z \quad (2)$$

where ρ is the water density at depth z, h is the total depth of the water column, and g is the gravitational constant. A greater amount of potential energy implies greater stability of the water column. Water temperature was profiled every metre with a YSI environmental 6920 probe (Anhydre, Vireux Molhain, France). Surface current velocities were measured once per second with a two-dimensional acoustic current meter probe (Falmouth Scientific Inc., Cataumet, Mass.) at a depth of about 0.5 m below the surface.

To characterize the influence of wind on the physical structure of the water column, and particularly on upwelling of hypolimnetic water, the dimensionless lake number L_N (Imberger and Patterson 1990) was calculated as follows:

$$L_N = \frac{\text{St}(H - h_T)}{u_*^2 A_S^{3/2}(H - h_V)} \quad (3)$$

where H is the total depth, h_T is the height from the bottom of the lake to the seasonal thermocline, h_V is the height from the bottom of the lake to the center of lake volume, and A_S is the surface area of the lake. The stability St was calculated as follows:

$$\text{St} = \frac{1}{\rho_0}\int_0^H g(h_V - z)\rho(z)A(z) \, \mathrm{d}z \quad (4)$$

where ρ_0 is the density of water, g is the acceleration due to gravity, and $A(z)$ and $\rho(z)$ are the area and the water density, respectively, at the height z. The water shear velocity induced by the wind u_* was calculated as follows:

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Fig. 1. Location of the study area and the sampling sites in Brittany, France. The wind rose summarizes local wind direction over four years (1999–2002) using Meteo France data.

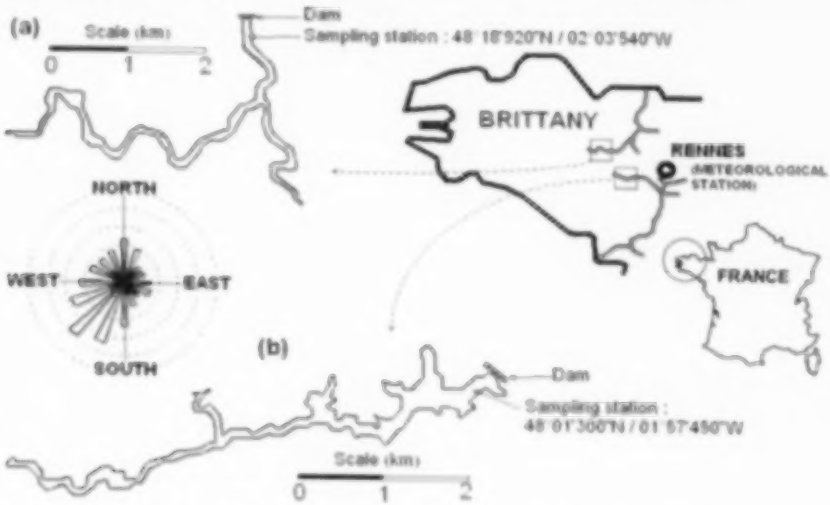

Table 1. Drainage basin and morphometric characteristics of the La Cheze and Rophemel reservoirs, France.

	La Cheze	Rophemel
Reservoir volume (10^6 m^3)	14.7	5
Surface area (km^2)	1.07	0.77
Mean depth (m)	13.7	6.5
Fetch (m) in predominant wind direction	900	120
Catchment area (km^2)	30	380
Water residence time	3 months to 1 year	1 week to 1 month

$$u_* = \left(\frac{C_D^S \rho_a}{\rho_0}\right)^{1/2} U \quad (5)$$

where ρ_a is the density of air, C_D^S is the surface drag coefficient, and U is the wind speed (m·s^{-1}).

Maximal water discharge was estimated from rainfall, multiplied by the surface of the catchment area. These values are approximate as they do not take into account evapotranspiration or infiltration but they give a useful indication of the extent of the rain impact on the lake volume.

To characterize the availability of light, daily average solar radiation was converted to mean photosynthetically active radiation (PAR), I_0, using a factor of 0.45 (Talling 1957). We then calculated the mean daily PAR, $\bar{I}_{Z_M}$, received by the phytoplankton over the mixed layer Z_M by integrating the light profile using the Beer–Lambert law:

$$\bar{I}_{Z_M} = \frac{1}{Z_M} \int_0^{Z_M} I_0 e^{-K_d z} dz \quad (6)$$

where K_d is the measured light attenuation coefficient, calculated from an instantaneous irradiance profile measured every metre with a LiCor PAR sensor (Eurosep Instruments, Cergy Pontoise, France).

To characterize nutrient availability at the four sampled depths, dissolved nutrient concentrations were also analysed through colorimetric methods: ammonium (Rossum and Villaruz 1963), nitrite and nitrate (Barnes and Folkard 1951), soluble reactive phosphorus (Murphy and Riley 1962), and silicon (Rodier 1978). Dissolved inorganic carbon was measured following filtration through a Whatman GF/F glass-fibre filter, using a total organic carbon analyser (Shimatzu TOC 5000; Shimatzu France, Champs-sur-Marne, France).

Species composition

To determine species composition of the phytoplankton community, subsamples (250 mL) containing cells from each of the four depths were concentrated on a 1 µm Poretics polycarbonate membrane filter, resuspended, and fixed with Lugol's iodine solution (final volume of 1 mL). Diatom chains and colonial chlorophytes were often observed, indicating that damage due to the concentration of cells was low. The alga taxa were identified according to standard references (Bourrelly 1966, 1968, 1970). All cells (both unicellular and cells grouped in filaments or colonies) were counted (magnification 100× to 400×) using a Nageotte chamber, and concentrations in the water column were expressed as cells per millilitre. Rare species low in concentration were taken into account only if the number of cells counted was sufficient for statistical significance: a minimum of 50 cells or colonies were thus counted per species to give confidence

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limits between 37 and 66 cells (Lund et al. 1958). The diversity index, rates of change, and statistical analyses were all based on data on cell concentrations, as outlined below.

Diversity index

To characterize the species diversity, the Shannon diversity index H' was calculated from the number of cells per millilitre, p_i, of each species following the widely used formula of Shannon (1948):

$$H' = -\sum_{i=1}^{S} (p_i \log_2 p_i) \quad (7)$$

Species rate of change

To characterize short-term modifications of the community structure, the succession rate of change σ (day^{-1}), also called the summed difference (SD) index, was calculated by adding together changes in proportions of the ith species between times t_1 and t_2 (Lewis 1978*a*; Cardoso and Marques 2003):

$$\sigma = \frac{\sum^{i} \left[\left[\frac{b_i(t_1)}{B(t_1)} \right] \left[\frac{b_i(t_2)}{B(t_2)} \right] \right]}{(t_2 - t_1)} \quad (8)$$

where b_i is the cell concentration of species i and B is the cell concentration per millilitre of the community.

Statistical analysis

To characterize the phytoplankton community according to seasons, in terms of dominant species and groups, a factorial correspondence analysis (CA) was undertaken. The analysis was performed on data from the four sampling periods using communities from the different dates and depths. The CA allowed us to highlight dominant species and gives an indication of the temporal and spatial variability of the community structure at the seasonal time scale.

Principal component analysis (PCA) was performed for each sampling period, separately on physical and chemical data and on species concentrations from each sampled depth and date. These two ordinations of species concentration and physical and chemical conditions were then compared with each other. From the results of the two PCA ordinations, a procrustean superimposition was performed (Dray et al. 2003*b*) to fit the two data sets in a euclidian multivariate space. The method minimizes a distance, which is the sum-of-squares of the differences between the two data sets in terms of variability (Peres-Neto and Jackson 2001). The residuals between configurations after optimal fit for each species are represented by the length of the arrows on the procrustean superimposition. The method thus draws a parallel between some environmental changes and some species concentration variations, so that it can associate a change in species concentration with an environmental change. The ordinations of the physical and chemical parameters and the species concentrations are shown, as well as the procrustean superimposition of both ordinations. To simplify figures, only species contributing to more than 1/S, where S is species richness, are shown, even if all species with statistically significant concentrations were included in the analysis. The fit between original data and the ordination of the common projection is measured by the sum of singular values of procrustean analysis (Dray et al. 2003*a*). A randomization test (the RV test; Heo and Gabriel 1997; Dray et al. 2003*b*) was used to evaluate the accuracy of the fit by the procrustean method, by randomly permuting rows and columns of one of the PCAs and calculating the new co-structure of the two PCAs matrices as explained above (1000 permutations). The better the fit, the stronger is the link between the two PCA matrices. Species that contribute most to the total variability of community structure also have the highest contributions to the axes and are not necessarily dominant species. All statistical analyses were performed using the ADE4 package of the R software (Kangas 2004).

Terminology

Three time scales were used: short term, a time scale of 2 or 3 days; intermediate, the 3-week sampling period; and seasonal, a few months.

Dominant species are the most abundant in the phytoplankton community and are statistically defined by the results of a CA. Rare species are species low in density, but their density was statistically significant (more than 50 cells or colonies counted) at least at a moment in the sampling period. We consider indicator species to be those for which cell concentration varies with change in physical or chemical conditions and can thus be indicative of an environmental change or disturbance. Indicator species were identified by the procrustean analysis.

Results

Physical and chemical forcing

The four sampling periods differed in their physical and chemical conditions, e.g., stratification intensity, water temperature, availability of light, and concentrations of nutrients (Table 2). Critical concentrations were used to characterize resource conditions above which phytoplankton species are unlikely to be limited by the resource. Below these concentrations, some of the species, particularly large species, may be limited, following the size dependance of resource acquisition (Irwin et al. 2006). We hypothesized that some rare species requiring higher nutrient concentration may increase their density in response to sudden nutrient release. These critical values were 10 µg P·L^{-1}, 0.3 mg N·L^{-1} (Wetzel 2001), and 0.5 mg Si·L^{-1} (Reynolds 1984*a*). Similarly, light was considered as potentially limiting for the growth of some of the phytoplankton species, when the mean light received by cells over the mixed layer was lower than 4 to 6 µmol photons·s^{-1}·m^{-2} (Millard et al. 1996). A deep, well-mixed, nutrient-rich, and light-limited epilimnion was characteristic of the sampling period of early spring at La Cheze. In late spring, the phytoplankton community at Rophemel was limited neither by nutrient nor by light because of an increase of solar radiation. A shallow silicon-depleted epilimnion characterized the summer period at La Cheze, whereas the phytoplankton community in autumn at the same site was potentially limited by both nutrients (silicon, nitrate, and phosphorus) and light (data not shown). More details are reported in Pannard et al. (2007).

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Table 2. Physical, chemical, and biological variables for each sampling period (data from Pannard et al. (2007); mean value ± standard deviation).

	Rophemel	La Cheze		
	Spring	Spring	Summer	Autumn
Physical constraints				
Potential energy ($J \cdot m^{-3}$) (water column)	10.7±3.9	3.5±1.7	55.5±8.5	28.1±5.8
Mean temperature (°C) (mixed layer)	15.2±1.8	9.1±0.9	22.5±0.9	16.8±0.9
Resources (mixed layer)				
Nitrate (mg $N \cdot L^{-1}$)	4.5±1.9	5.6±1.1	2.6±1.3	0.1±0.1
Ammonium (μg $N \cdot L^{-1}$)	3±4	65±14	93±13	28±13
Phosphate SRP (μg $P \cdot L^{-1}$)	43±19	42±5	16±3	6±9
Silica (mg $Si \cdot L^{-1}$)	3.5±0.6	1.1±0.2	0.3±0.1	0.4±0.2
Irradiance (μmol photons·$m^{-2} \cdot s^{-1}$)	11.6±4.8	2.5±0.9	15.2±7.6	1.3±1.0
Chlorophyll *a* (μg Chl $a \cdot L^{-1}$) (mixed layer)	13.1±3.7	4.7±1.2	3.9±1.0	6.6±0.5
Mean sedimentary fluxes ($g \cdot m^{-2} \cdot day^{-1}$)	6.4±1.9	2.6±0.7	2.2±1.1	8.3±5.4

Temperature and solar radiation also underwent gradual variations over the 3 weeks of each sampling period because of seasonal transitions and meteorological forcing such as atmospheric depression. These variations were reflected in the evolution of the mean temperature of the mixed layer and the intensity of stratification during the 3-week sampling periods and had thus to be taken into account in the phytoplankton response.

Pannard et al. (2007) demonstrated in the same study that between two and three short-term forcing events occurred per 3-week sampling period, with physical and chemical modifications of different intensity. Three main physical and chemical modifications of the environment dominated within the sampling periods: an increase of dilution rate, a sudden increase of stratification intensity due to a spring warming-up (associated with a change in mixed-layer depth), and an input of potentially limiting nutrients (Pannard et al. 2007). Firstly, the phytoplankton community of Rophemel was exposed to heavy rain (Fig. 2*a*), which increased dilution rate of populations in the reservoir mainly on day 7. Secondly, the early spring community of La Cheze was exposed, particularly on day 10, to a strong wind event (with mean daily wind speed up to 7 $m \cdot s^{-1}$) associated with higher solar radiation, which induced a warming-up of the reservoir and increased the stratification intensity, resulting in an increase of the lake number above 1 (Fig. 2*b*). Thirdly, in autumn at La Cheze, a rainfall event on day 7 (Fig. 2*d*) induced a silicon input into the mixed layer, increasing it from 0.58 to 1.36 mg $Si \cdot L^{-1}$. A 5-day wind event just followed the rain event and was associated with a measurable increase in the availability of phosphorus on days 12 to 16, increasing it from below 1 μg $P \cdot L^{-1}$ to 22 μg $P \cdot L^{-1}$. However the lake number always greatly exceeded the critical value of 1 (Fig. 2*d*). No sudden physical and chemical modification of the environment was observed during the fourth sampling period, the summer period at La Cheze. The lake number remained greatly higher than 1 during the entire period, and only very little rainfall occurred (Fig. 2*c*).

Diversity index and rate of change of the phytoplankton community

Mean values of H' were calculated for sampling period and at the top three sampled depths, as we considered that the vertical structure of diversity could provide information about the community response at the water column scale (Fig. 3*a*). The lowest values were observed at Rophemel, with an average over the 3-week period and the three sampled depths of 1.82 ± 0.75 (mean ± standard deviation; n = 7), whereas H' at La Cheze was 2.95 ± 0.14 (n = 8) in April, 3.32 ± 0.24 (n = 9) in October, and 4.04 ± 0.20 (n = 7) in June. These diversity indices increased with the stratification intensity and the mean temperature of the mixed layer (Table 2). The diversity indices were also strongly correlated with the potential energy during the warming period in Rophemel in spring and the cooling period in La Cheze in autumn (Fig. 4). The other two sampling periods showed lower variations (and correlations) of temperature and potential energy (Fig. 4). A positive relation between the diversity index and the stratification intensity was thus observed on two time scales (seasonal and intermediate). However, on a daily time scale, the diversity index H' changed only gradually (Fig. 3*a*). The diversity index H' was thus not sensitive to physical forcing on a daily time scale but was sensitive to seasonal forcing such as that resulting from stratification and temperature.

Rates of community change were highly variable on a daily time scale compared with diversity indices, although mean values, averaged over dates and depths for each sampling period, were very close to one another, between 0.22 and 0.3 (Fig. 3*b*). This rate of change was not influenced by seasonal forcing, but on a daily time scale, it was controlled by the occurrence of forcing events, increasing after disturbances (Fig. 3*b*). This increase was sometimes observed only at the surface, e.g., sampling of Rophemel and La Cheze in June, sometimes at a depth of 7 m, as in October, and sometimes at the top three depths, as in April (Fig. 3*b*). This parameter was thus a good indicator of rapid change due to forcing on a daily time scale. We now examine the extent of change in the relative concentrations of species after forcing events.

Community structure

On seasonal and intermediate time scales, dominant species differed between the four sampling periods (Fig. 5). Large diatoms such as *Aulacoseira* sp. dominated the cold, well-mixed, light-limited waters in early spring at La Cheze

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Fig. 2. Temporal pattern of lake number L_N (open squares) and maximal water discharge (solid diamonds) in (*a*) Rophemel reservoir and (*b*–*c*) La Cheze reservoir in (*b*) early spring, (*c*) summer, and (*d*) autumn. Horizontal broken lines indicate the critical value of L_N below which we consider there is upwelling of hypolimnetic water during the wind episode.

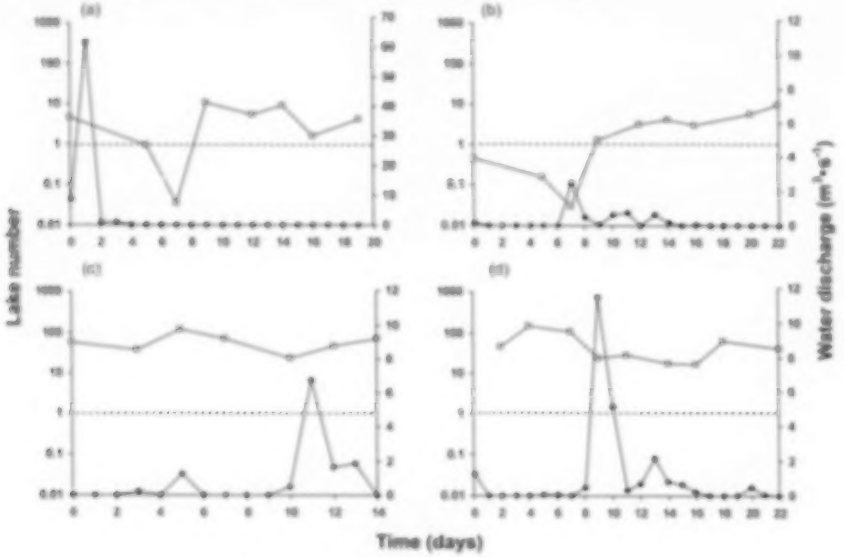
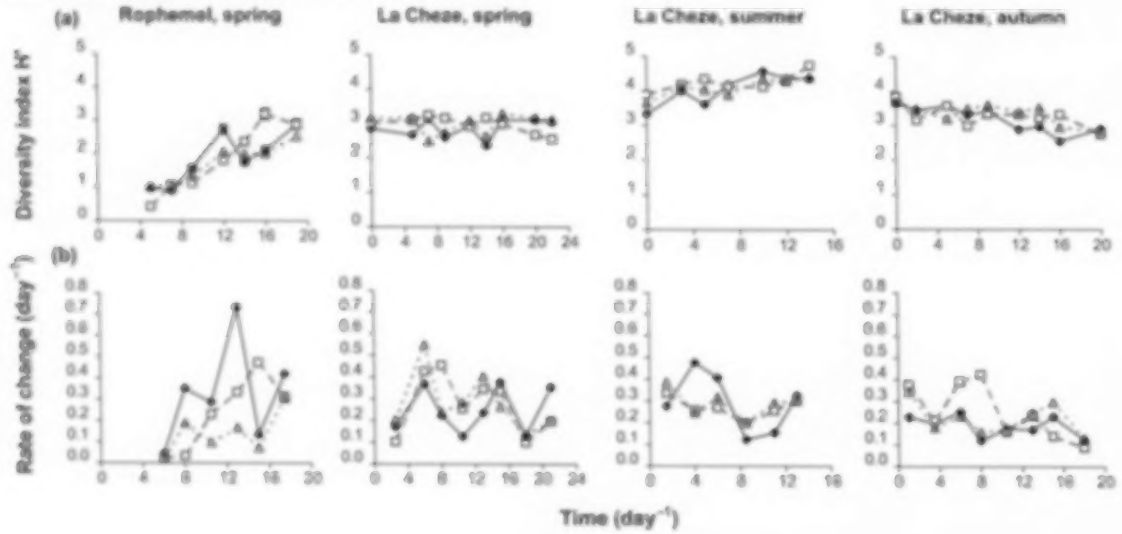


Fig. 3. Temporal patterns of (*a*) diversity index H' and (*b*) the rate of change for each sampling period and each sampled depth: 1 m (solid diamonds and solid lines), 5 m (Rophemel) or 7 m (La Cheze) (open squares and broken lines), and 9 m (Rophemel) or 13 m (La Cheze) (open triangles and dotted lines).



and at the beginning of the sampling period of Rophemel, whereas chlorophytes and cyanobacteria dominated the stratified, nutrient-depleted surface in summer and early autumn at La Cheze (Fig. 5; Table 2). In the short term, the concentration of some species that did not necessarily dominate the community could also be modified, as shown by the procrustean analysis (Figs. 6–9).

The procrustean analysis of Rophemel in spring (RV = 0.514, $p < 0.001$) highlighted a temporal variability in the physical and chemical environment and in the phytoplankton community structure, with forcing factors and biological response on day 5 as one side of the first axis and forcing factors and biological response on days 14, 16, and 19 on the other side (Fig. 6c). The physical and chemical parameters that contributed to the first axis of the first PCA were nitrate (37.8%), silica (24.4%), and temperature (15.9%) (Fig. 6a). The contributing species to the second PCA were diatoms such as *Navicula* sp. (11.7%), *Aulacoseira* sp. (8.6%),

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Fig. 4. Diversity index *H'* as a function of potential energy for each sampling period; correlations between both parameters are shown when highly significant.

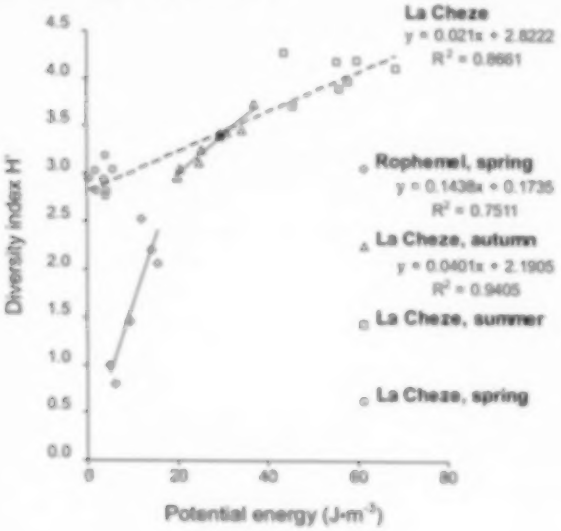
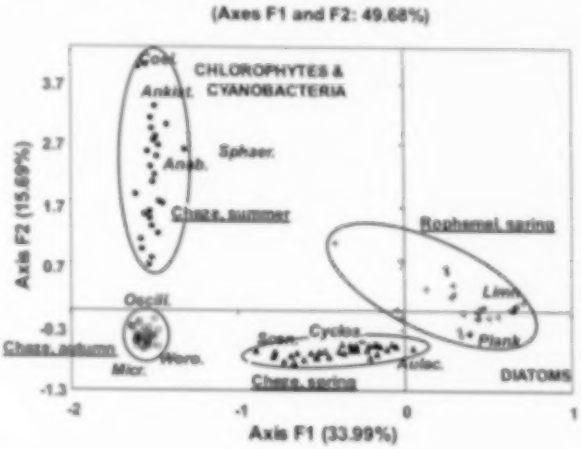


Fig. 5. Principal component analysis of the species composition used to highlight dominant species (contributing species to the axis). The dominant species belong to chlorophytes (*Ankist.*, *Ankistrodesmus*; *Coel.*, *Coelosphaerium*; *Scen.*, *Scenedesmus*; *Sphaer.*, *Sphaerocystis*), cyanobacteria (*Anab.*, *Anabaena*; *Limn.*, *Limnothrix*; *Micr.*, *Microcystis*; *Oscill.*, *Oscillatoria*; *Plank.*, *Planktothrix*; *Woro.*, *Woronichinia*), and diatoms (*Aulac.*, *Aulacoseira*; *Cyclos.*, *Cyclostephanos*).



Cyclostephanos sp. (6.0%), and *Synedra* sp. (6.0%), chlorophytes such as *Scenedesmus* sp. (9.9%), or cyanobacteria such as *Planktothrix* sp. (7.4%) (Fig. 6*b*). All of these species decreased following the environmental change, a sudden increase in the water column stratification intensity. The contributing species favoured by the environmental change were colonial chlorophytes *Coelastrum* sp. (9.3%) and *Pediastrum* sp. (5.6%) (Fig. 6*b*). In the procrustean analysis, surface communities (1 and 5 m deep represented by the letters A and B, respectively) were on one side of the second axis of both PCAs and bottom communities (9 and 14 m deep represented by the letters C and D, respectively) were on the opposite side (Fig. 6*c*). The physical and chemical parameters that contributed to this second axis of the first PCA were ammonium (25.6%), light availability (mean PAR) over the mixed layer (23.9%), and temperature (13.5%) (Fig. 6*a*). Contributing species were the colonial chlorophytes *Sphaerocystis* sp. (18.4%), *Coelastrum* sp. (12.5%), and *Pediastrum* sp. (12.3%) (Fig. 6*b*). The shift, occurring on day 7 and associated with a dilution induced by a large rain event, led to the disappearance of many species, particularly diatoms, which were replaced by new ones, mainly colonial chlorophytes.

The procrustean analysis for the period of early spring at La Cheze (RV = 0.313, $p = 0.007$) also highlighted a temporal variability, observed both in the physical and chemical environment and in the community structure (Fig. 7*c*). Sampling dates before the strongest wind event (day 10) can be distinguished from sampling dates after the disturbance (Fig. 7*c*). Silicon (37.8%), temperature (27.4%), inorganic carbon (21.6%), and nitrate (10.4%) were the main variables contributing to the first axis of the PCA of the physical and chemical parameters (Fig. 7*a*). Temperature and nitrate were increased following the disturbance. Large diatoms such as *Aulacoseira* sp. (14.4%) and *Synedra* sp. (9.0%) were replaced by smaller diatoms such as *Cyclotella* sp. (22.9%) (Fig. 7*b*). Some cyanobacteria and chlorophytes were also favoured by the increase in temperature and water column stratification intensity, e.g., *Aphanizomenon* sp. (8.4%) and *Sphaerocystis* sp. (7.6%) (Fig. 7*b*). Surface community could not be distinguished from bottom community in the procrustean analysis, indicating no depth-related variations in spring.

A spatial variability related to depth was observed in the procrustean analysis for the summer period at La Cheze (RV = 0.547, $p < 0.001$), with surface samples on the right side of the graph (depths of 1 and 7 m represented by letters A and B, respectively) and bottom samples on the left side (depths of 13 and 21 m represented by letters C and D, respectively) (Fig. 8*c*). The vertical structure of phytoplankton communities thus dominated over temporal changes. Physical and chemical parameters that were dependent on depth were temperature (34.7%), silicon (22.4%), current velocity (17.7%), and light availability over the mixed layer (14%) (Fig. 8*a*). Contributing species were *Anabaena* sp. (14.7%), *Monoraphidium* sp. (14.3%), *Botryococcus* sp. (12.6%), and *Coelosphaerium* sp. (9.8%), with higher concentrations in the surface layer (Fig. 8*b*). The second axis of the procrustean analysis was not linked to time or to the occurrence of forcing events and the inertia of the axis remained low compared with the first axis, as shown by its eigenvalue, which was five times lower (Fig. 8).

During the autumn period, vertical structuring also dominated, as shown by the procrustean analysis (RV = 0.462, $p < 0.001$), with surface samples (depths of 1 and 7 m represented by letters A and B, respectively) on the right side of the graph and bottom ones (depths of 13 and 21 m represented by letters C and D, respectively) on the left side

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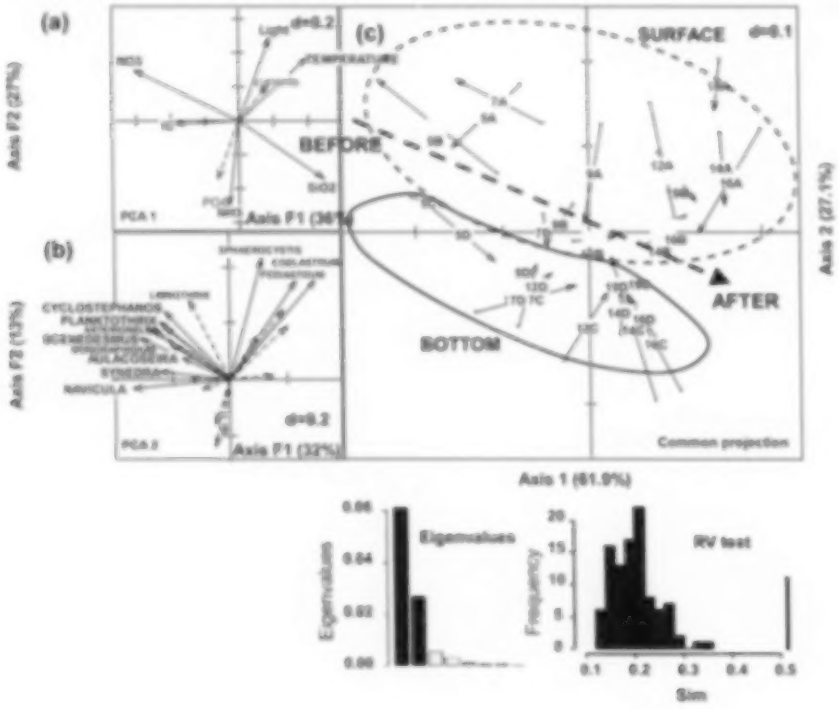
Figs. 6–9. Procrustean analysis with (*a*) PCA of the physical and chemical conditions (temperature, inorganic carbon (IC), silicon (SiO2), phosphorus (PO4), ammonium (NH4), nitrate (NO3), current velocity (currents), and mean irradiance in the mixed layer (Light)), (*b*) PCA of the species composition, with indicator species written in larger characters than other species, and (*c*) common projection. Solid arrows on the PCA indicate physical and chemical parameters or species, which significantly contribute to one of the two axis (compared with dotted arrows). In (*a*, *b*, and *c*), the *d* value indicates the size of the square for each ordination. In (*c*), the letters A, B, C, and D represent the four sampled depths (see each figure legend) and are preceded by the time in days from the beginning of the period. The small solid arrows in (*c*) show the change in the location of each date and depth between the structure of physical and chemical parameters and the community structure. The large broken arrow in (*c*) represents the mean modification of the community structure. Circles are used when possible to group together communities from the surface (broken circles), from the bottom (solid circles), or from the same period (double-line circles), with indication of the group nearby. Histograms of eigenvalues are shown in the bottom of the figure, with the first two solid bars representing the first two axes. The results of the randomization test are shown in the bottom right histogram, with the observed RV coefficient value represented by the vertical line. **Fig. 6.** Procrustean analysis of Rophemel in spring. In (*c*), the letters A, B, C, and D represent the four sampled depths 1, 5, 9, and 14 m, respectively.



(Fig. 9*c*). The first axis of the PCA of the physical and chemical variables thus coincides with depth, temperature (35.2%), light availability over the mixed layer (25.1%), and inorganic carbon (20.0%), the main contributing physical and chemical variables (Fig. 9*a*). *Botryococcus* sp. (9.4%), *Tetraedron* sp. (8.7%), *Nephrocytium* sp. (6.3%), *Aulacoseira* sp. (5.9%), and *Asterionella* sp. (5.7%) were the main species contributing to the first axis of the PCA of community structure (Fig. 9*b*). The procrustean analysis also distinguished sampling dates before the 5-day wind event (highest wind speed on day 12) on the upper side of the second axis and sampling dates after on the bottom side (Fig. 9*c*). The second axis thus coincides with time and wind disturbance, with phosphorus (32.9%) and silicon (26.3%) as the main contributors to the short-term environmental change (Fig. 9*a*). The contributing species, which decreased following the disturbance, were *Pseudanabaena* sp. (8.3%), *Selenastrum* sp. (7.3%), and *Cosmarium* sp. (6.9%). Large diatoms such as *Aulacoseira* sp. (6.3%) and chlorophytes such as *Coelastrum* sp. (5.7%) were favoured by nutrient inputs (Fig. 9*b*). A shift in the community structure was thus observed in parallel with a change in nutrient availability.

Discussion

Depending on forcing events, modifications of the community structure were variable and induced by a change in the availability of resources or in the intensity of stratification. Shifts in the community occurred over a few days, during and following disturbances, and no return to the original community structure was observed. In several of the sampling periods, a gradual change of physical and chemical conditions occurred on a weekly time scale, as shown by Pannard et al. (2007), leading to significant modifications of the phytoplankton community between the beginning and the end of the sampling period. Forcing affected light and nutrient avail-

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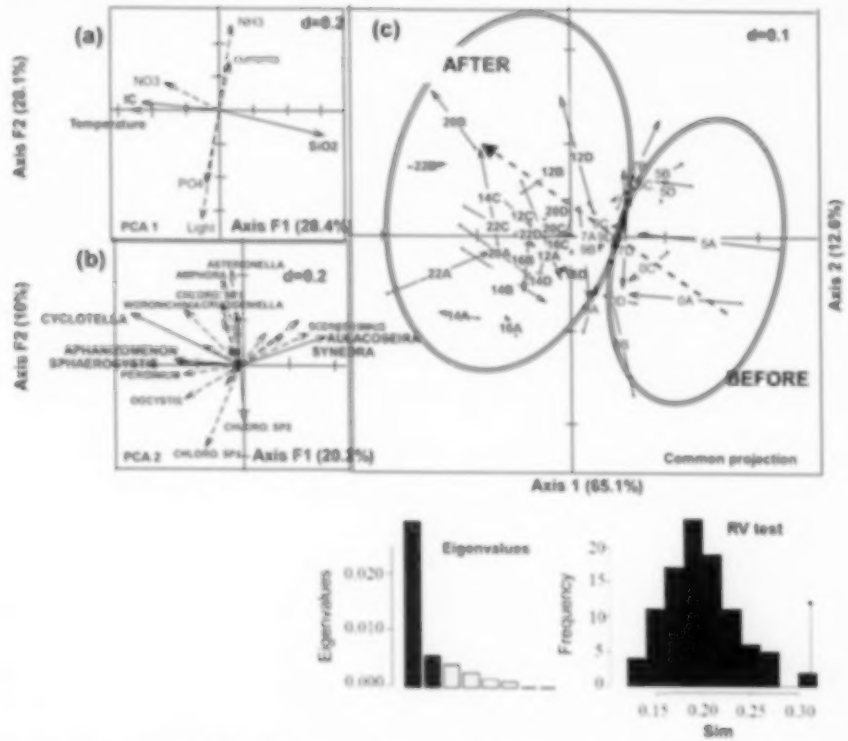
Fig. 7. Procrustean analysis of La Cheze in early spring. In (*c*), the letters A, B, C, and D represent the four sampled depths 1, 7, 13, and 21 m, respectively.



ability and stratification intensity at different time scales, which were in turn reflected in phytoplankton dynamics (Fig. 10). Seasonal modification of the phytoplankton community structure (represented by the large solid arrow in Fig. 10) shows change in the concentration of dominant groups (cyanobacteria, diatoms, and chlorophytes) and in the diversity index. Modifications on a time scale of a few weeks, represented by the small solid arrow (Fig. 10), show similar changes to seasonal modifications, but to a lesser extent, observed over the time scale of the sampling period, whereas shifts in the phytoplankton community on a time scale of a few days, represented by the small dotted arrow (Fig. 10), characterize changes in concentration of indicator species and in species turnover.

Initial community structure: a response to seasonal forcing

The community in place (i.e., the dominant species) changed with season, being mainly diatoms during the nutrient-repleted and well-mixed conditions and mainly cyanobacteria and chlorophytes during the stratified period. The community structure, in terms of dominant species, may be regarded as a response to the seasonal forcing. The initial community structure may influence the response to short-term physical forcing, as the initial conditions and competing species that make up the community represent key factors affecting the outcome of competition (Huisman and Weissing 1999). The response to disturbance will thus change with season.

Short-term physical forcing and community responses

During and following the sudden environmental changes, indicator species responses occurred over time scales of a few days. Following a rainfall event in Rophemel reservoir in late spring, a transition between large diatoms and colonial chlorophytes was observed on a time scale of a few days. This transition was in accordance with expectations from phytoplankton succession (Garnier et al. 1995). The higher growth rate of chlorophytes, about twice that of diatoms, may have been an advantage that counteracted the higher dilution rate associated with heavy rainfall.

The absence of return to the original community structure at the end of the sampling period is probably due to forcing on the intermediate time scale from changes in air temperature and solar radiation, which increased the intensity of stratification, water temperature, and light availability. Diatoms underwent higher loss by sedimentation following the disturbance, so that the populations could not be sustained, as discussed in Huisman et al. (2002). Conditions thus became more favourable for chlorophytes.

During the period of high nutrient availability in spring at La Cheze, a shift in terms of indicator species was induced by a sudden increase in the intensity of stratification and of temperature in the mixed layer. During the nutrient-replete, well-mixed, low-light conditions, large diatoms dominated the phytoplankton community in accordance with previous studies (Anneville et al. 2002), but they were replaced by a smaller diatom species following the short-term environmen-

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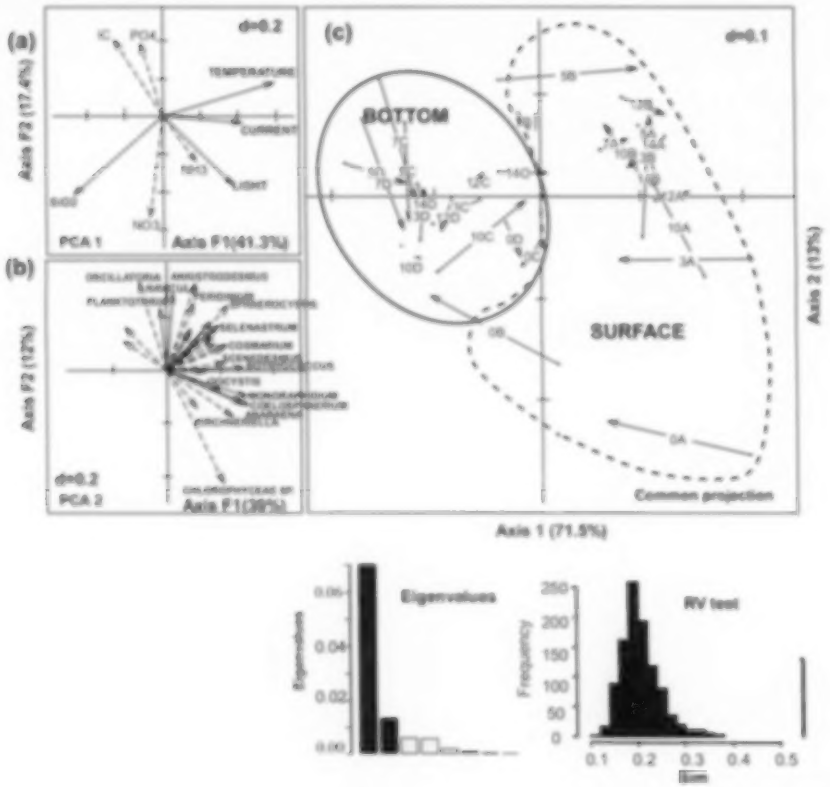
Fig. 8. Procrustean analysis of La Cheze in early summer. In (c), the letters A, B, C, and D represent the four sampled depths 1, 7, 13, and 21 m, respectively.



tal change. The increase of the intensity of stratification was thus disadvantageous to large diatoms, which undergo higher loss rates by sedimentation than small diatoms in accordance with Stokes law and which require a higher mixing rate to stay in suspension.

In early autumn at La Cheze, the shift in terms of indicator species was associated with a double pulse of silicon and phosphorus at a 2-day interval in a community initially limited both by these nutrients and by light. The modification of the phytoplankton community was probably due not to external input of populations, but rather to an internal redistribution of nutrients, as species that increased, e.g., *Synedra* sp. and *Aulacoseira* sp., were already present in the water column before the disturbance, through in low concentrations. Moreover, some species were not influenced by the occurrence of the forcing events, e.g., *Oscillatoria* sp. Responses thus varied with species. Lastly, we estimated the mean growth rate from differences in species concentrations between two dates and for each depth. Mean growth rate remained plausible with values always smaller than 1-day^{-1}. We therefore favour the internal redistribution of nutrients and the shift in the community structure hypothesis.

In a community dominated by chlorophytes and cyanobacteria, the forcing events promoted the increased concentration of large colonial diatoms, with a peak of concentration on day 14. The absence of return to the original community structure, in terms of indicator species, was also due to forcing on the intermediate time scale with the autumnal decrease of water temperature and light availability, which was disadvantageous to several species of cyanobacteria and chlorophytes.

Regardless of the induced environmental changes, the same response of the community was observed: over a few days, some species were replaced by indicator species, always in the direction of the seasonal succession, leading to an increase in the rate of turnover of species without a shift back to the original community. One could argue that forcing events should induce a short successional episode followed by a reversion of the seasonal succession after the events, as observed in tropical Lake Lanao, where Lewis (1978*b*) observed a series of successional episodes initiated by abrupt environmental changes, generally nutrient inputs, that induced a return to the early stage of the succession. The higher irregularity of resource supply in tropical lakes compared with temperate ones (Lewis 1978*b*) may lead to the return to an early stage of succession. In our case, the modifications of the communities after a short-term environmental change remained in the direction of the seasonal succession, which proceeded as a series of short-term physical forcings.

Resistance to short-term physical forcing induced by stratification

No shift of phytoplankton communities was observed during the strong stratification period of summer when the

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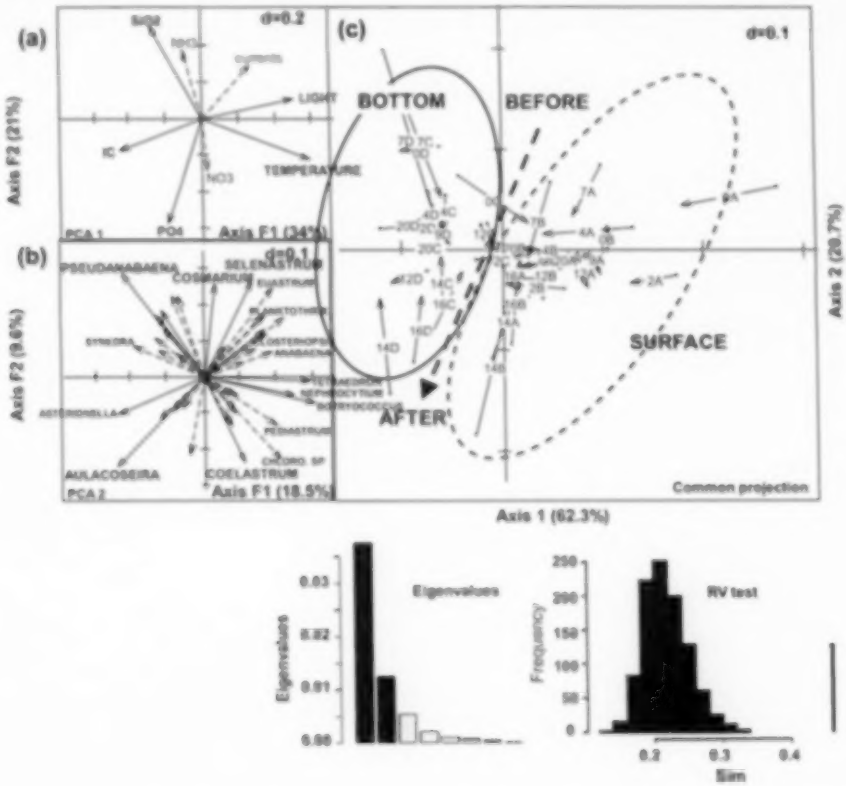
Fig. 9. Procrustean analysis of La Chaise in autumn. In (*c*), the letters A, B, C, and D represent the four sampled depths 1, 7, 13, and 21 m, respectively.



water column was strongly stratified. During the summer period, two wind events occurred that led to a small increase of the mixed-layer depth (Pannard et al. 2007), but the wind events were not sufficient to affect L_S. The high stratification intensity of the water column and the lack of a nutrient pulse may explain the absence of response of the community structure in terms of indicator species.

The vertical segregation of phytoplankton community associated with the stratification can thus influence the response of phytoplankton community. In spring, particularly in early spring, as opposed to summer and autumn, the water column was mixed, as shown by the low potential energy, so that no vertical structuring of the phytoplankton community occurred. Consequently, only the surface community responded to forcing events when the water column was stratified, whereas both surface and bottom communities were affected when the stratification was weak, as indicated by the increase of the rate of change following disturbance events at all depths in spring and only in the surface mixed layer in summer.

Diversity index and rate of community change

The evolution of the community structure, demonstrated through multivariate analysis, indicated sensitivity to all species, whereas the two indices diversity and rate of change were, by definition, sensitive to the evolution of dominant species. Values of the diversity index between the different sampling periods and lakes are close to values given in the literature, often 3 or 4 (Huszar and Reynolds 1997; Padisák et al. 1998). However, the values of the rate of change between the different sampling periods and lakes were high, exceeding 0.1·day^{-1} (Lewis 1978*a*). Values higher than 0.1·h^{-1} have been observed in a shallow lake (Cardoso and Marques 2003) where resuspension associated with wind induced these rapid changes.

The two indices diversity and rate of change were complementary as they were controlled by different time scales of physical and chemical forcing. The diversity index is found to be a good indicator of a biological response to forcing on a seasonal and intermediate time scale, as it is mainly controlled by stratification, whereas the rate of change is a good indicator of short-term forcing events on a daily time scale.

The link observed between the stratification intensity and the diversity index may be indirect, as the intensity of the stratification represents a good proxy of temperature and seasonal cycle. The diversity increased during the year, as the temperature increased. However, one would need further investigation (in particular sampling throughout the year and later in the autumn) to be more confident of the observed relation between diversity index, temperature, and seasonal succession.

Shifts in the community structure were not reflected in the diversity index; it was the rate of change that highlighted shorter-term community responses. We had expected that forcing events would also modify the diversity index, in par-

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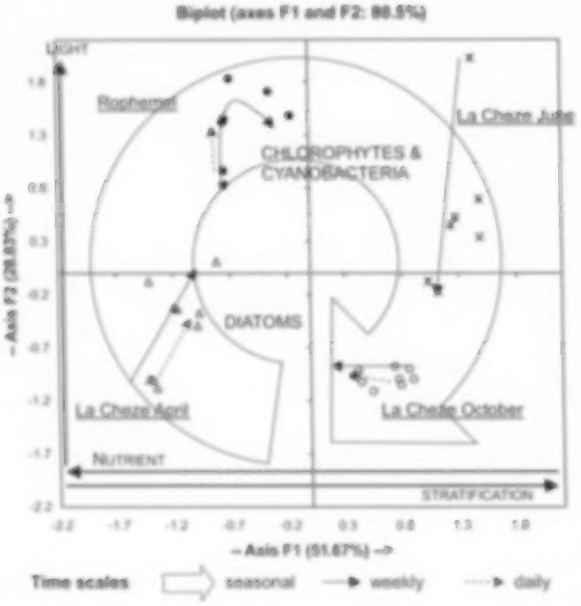
Fig. 10. Summary of changes in phytoplankton communities over seasonal, weekly, and daily time scales (the arrows represent phytoplankton response to each forcing).



ticular when a shift in community structure was observed. However, species that decreased in concentration were replaced by other species in such a way that all niches were always occupied and, thus, diversity remained about the same. Moreover, we expected the diversity index H' to show greater fluctuations, being calculated using cell abundances. Indeed, changes in the concentration of colonial species were responsible for high variations of the index and may have affected it too strongly (Figueredo and Giani 2001). Despite using cells as the ecological unit, the diversity indices did not show fluctuations, whereas most of the forcing events induced, at least in the surface layer, an increase of the successional rate of change. In several cases, in particular in summer, the rate of change thus increased in the surface layer without a change in the species composition in terms of indicator species. This discrepancy may be explained by an oversensitivity of the parameter: the rate of change is the sum of the differences in the proportion of each species between two sampling dates, so that a modification in the concentration of a dominant species, such as large colonial ones, can affect the proportions of all other species. Large colonial species are mainly represented by cyanobacteria, which are disfavoured by mixing (Reynolds 1984*a*). Forcing events may affect populations of colonial species, with repercussions on the index rate of change, even if the community species structure did not really change significantly.

We demonstrated that wind disturbances can induce modifications of phytoplankton community on a daily time scale, both in terms of size structure (Pannard et al. 2007) and species composition. Through temporal variability of the environmental conditions, short-term physical forcing may decrease competitive exclusion and thus increase species diversity (Grover 1988), even if in our study, the diversity index was not increased by the occurrence of disturbances. For example, it was demonstrated that disturbances such as an artificial deepening of the mixed layer in enclosures leading to a higher nutrient availability increased the diversity of phytoplankton in a lake with a very stable stratification, in particular with a disturbance frequency of 6 days (Flöder and Sommer 1999). In that study, undisturbed communities were compared with disturbed ones at different frequencies, where the highest value of H' was between 2.5 and 3. In our study, the phytoplankton communities changed in response to a natural pattern of disturbances, with about one forcing event per week and one large forcing event per sampling period. Changes in the diversity index may have been masked by modifications of the community by species replacement.

Forcing events may thus be seen as intermediate disturbances for the phytoplankton community (Reynolds 1988), sensu Connell's intermediate disturbance hypothesis (1978). This hypothesis postulates that disturbance opens space for colonization. On an intermediate frequency of disturbances, the community is composed of a mosaic of patches at different stages of succession so that species richness at the community level is the highest (Ricklefs and Miller 1999). With more frequent disturbances, many populations do not persist, whereas with less frequent disturbances, the mosaic of patches disappears, leading to competitive exclusion. However, the phytoplankton communities in our study change over three time scales in response to physical forcing, from a time scale of a few days to weekly and seasonal time scales. Consequently, successive disturbances affected different communities, and the species that are considered as indicators for the following disturbance may be different ones. This is also observable on the seasonal time scale, in which the initial composition of the communities is quite different, in particular with respect to the dominant group (diatoms, cyanobacteria). As the phytoplankton community changes following seasonal succession, disturbances by wind or rain events will accelerate the transitions between dominant groups, but they will not favor their codominance or increase the diversity of the community. Therefore such events were not considered here as intermediate disturbances. In sum, the phytoplankton community is seen to be embedded in a hierarchical pattern of forcing events, with short-term events accelerating community changes towards seasonal succession, which in turn responds to forces evolving over a longer time scale.

This study has shown that three time scales of physical and chemical forcing induced different responses in the phytoplankton community in terms of diversity, successional rate of community change, dominant species, and indicator species. The successional rate of change was the most sensitive response parameter to the occurrence of short-term forcing events, whereas the diversity index was most sensitive to seasonal and intermediate forcing, in particular to the stratification intensity. Most of the forcing events, while increasing the rate of change, did not induce a change in the phytoplankton community structure or in the concentration of indicator species. Only multivariate analysis of the community structure revealed that a shift in community had oc-

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curred. Moreover, the community did not revert to the initial community after the disturbance because of intermediate time scale forcing having modified the background physical and chemical conditions. Short-term forcing accelerated species turnover with shifts in the phytoplankton community over a few days, always in the direction of the seasonal succession because of the intermediate time scale of forcing.

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References

Anneville, O., Souissi, S., Ibanez, F., Ginot, V., Druart, J.-C., and Angelli, N. 2002. Temporal mapping of phytoplankton assemblages in Lake Geneva: annual and interannual changes in their patterns of succession. Limnol. Oceanogr. **47**(5): 1355–1366.

Barnes, H., and Folkard, A.R. 1951. The determination of nitrite. Analyst, **76**: 599–603.

Bourrelly, P. 1966. Les algues d'eau douce. I. Les algues vertes. Boubee & Cie, Paris, France.

Bourrelly, P. 1968. Les algues d'eau douce. II. Les algues jaunes et brunes. Boubee & Cie, Paris, France.

Bourrelly, P. 1970. Les algues d'eau douce. III. Les algues bleues et rouges. Boubee & Cie, Paris, France.

Cardoso, L.S., and Marques, D.M. 2003. Rate of change of the phytoplankton community in Itapeva Lake (north coast of Rio Grande do Sul, Brazil), based on the wind driven hydrodynamic regime. Hydrobiologia, **497**(1–3): 1–12.

Connell, J.H. 1978. Diversity in tropical rain forests and coral reefs. Science (Washington, D.C.), **199**: 1302–1310.

Diehl, S., Berger, S., Ptacnik, R., and Wild, A. 2002. Phytoplankton, light and nutrients in a gradient of mixing depths. Theor. Ecol. **83**(2): 386–398.

Dray, S., Chessel, D., and Thioulouse, J. 2003*a*. Co-inertia analysis and the linking of ecological data tables. Ecology, **84**(11): 3078–3089.

Dray, S., Chessel, D., and Thioulouse, J. 2003*b*. Procrustean co-inertia analysis for the linking of ecological tables. Ecoscience, **10**: 110–119.

Figueredo, C.C., and Giani, A. 2001. Seasonal variation in the diversity and species richness of phytoplankton in a tropical eutrophic reservoir. Hydrobiologia, **445**(1–3): 165–174.

Flöder, S., and Sommer, U. 1999. Diversity in planktonic communities: an experimental test of the intermediate disturbance hypothesis. Limnol. Oceanogr. **44**(4): 1114–1119.

Garnier, J., Billen, G., and Coste, M. 1995. Seasonal succession of diatoms and Chlorophyceae in the drainage network of the Seine River: observations and modeling. Limnol. Oceanogr. **40**(4): 750–765.

Grover, J. 1988. Dynamics of competition in a variable environment: experiments with two diatom species. Ecology, **69**(2): 408–417.

Heo, M., and Gabriel, K.R. 1997. A permutation test of association between configurations by means of the RV coefficient. Commun. Stat. Simulation Computation, **27**: 843–856.

Huisman, J., and Weissing, F.J. 1999. Biodiversity of plankton by species oscillations and chaos. Nature (London), **402**(6760): 407–410.

Huisman, J., Arrayas, M., Ebert, U., and Sommeijer, B. 2002. How do sinking phytoplankton species manage to persist? Am. Nat. **159**(3): 245–254.

Huisman, J., Sharples, J., Stroom, J., Visser, P., Kardinaal, W., Verspagen, J., and Sommeijer, B. 2004. Changes in turbulent mixing shift competition for light between phytoplankton species. Ecology, **85**: 2960–2970.

Huszar, V.L.d.M., and Reynolds, C.S. 1997. Phytoplankton periodicity and sequences of dominance in an Amazonian flood-plain lake (Lago Batata, Pará, Brasil): responses to gradual environmental change. Hydrobiologia, **346**(1–3): 169–181.

Imberger, J., and Parker, G. 1985. Mixed layer dynamics in a lake exposed to a spatially variable wind field. Limnol. Oceanogr. **30**(3): 473–488.

Imberger, J., and Patterson, J.C. 1990. Physical limnology. Adv. Appl. Mech. **27**: 303–475.

Irwin, A.J., Finkel, Z.V., Schofield, O.M.E., and Falkowski, P.G. 2006. Scaling-up from nutrient physiology to the size-structure of phytoplankton communities. J. Plankton Res. **28**(5): 459–471.

Kangas, M. 2004. R: a computational and graphics resource for ecologists. Front. Ecol. Environ. **2**(5): 277–277.

Klausmeier, C.A., and Litchman, E. 2001. Algal games: the vertical distribution of phytoplankton in poorly mixed water columns. Limnol. Oceanogr. **46**(8): 1998–2007.

Lagadeuc, Y., Brylinski, J., and Aelbrecht, D. 1997. Temporal variability of the vertical stratification of a front in a tidal Region Of Freshwater Influence (ROFI) system. J. Mar. Syst. **12**: 147–155.

Lewis, W. 1978*a*. Analysis of succession in a tropical phytoplankton community and a new measure of succession rate. Am. Nat. **112**(984): 401–414.

Lewis, W. 1978*b*. Dynamics and succession of the phytoplankton in a tropical lake: Lake Lanao, Philippines. J. Ecol. **66**: 849–880.

Lund, J., Kipling, C., and Cren, E.L. 1958. The inverted microscope method of estimating algal numbers and the statistical basis of estimations by counting. Hydrobiologia, **11**: 143–170.

MacIntyre, S., Flynn, K.M., Jellison, R., and Romero, J.R. 1999. Boundary mixing and nutrient fluxes in Mono Laka, California. Limnol. Oceanogr. **44**(3): 512–529.

Millard, E., Myles, D., Johannsson, O., and Ralph, K. 1996. Seasonal phosphorus deficiency of Lake Ontario phytoplankton at two index stations: light versus phosphorus limitation of growth. Can. J. Fish. Aquat. Sci. **53**: 1112–1124.

Murphy, J., and Riley, J.P. 1962. A modified single-solution method for the determination of phosphate in natural waters. Anal. Chim. Acta, **27**: 31–36.

Noges, T., Kisand, V., Noges, P., Pollumae, A., Tuvikene, L., and Zingel, P. 1998. Plankton seasonal dynamics and its controlling factors in shallow polymictic eutrophic Lake Vortsjarv, Estonia. Int. Rev. Hydrobiol. **83**(4): 279–296.

Padisák, J., Krienitz, L., Scheffler, W., Koschel, R., Kristiansen, J., and Grigorszky, I. 1998. Phytoplankton succession in the oligotrophic Lake Stechlin (Germany) in 1994 and 1995. Hydrobiologia, **369/370**: 179–197.

Pannard, A., Bormans, M., and Lagadeuc, Y. 2007. Short-term variability in physical forcing in temperate reservoirs: effects on phytoplankton dynamics and sedimentary fluxes. Freshw. Biol. **52**: 12–27.

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Peres-Neto, P.R., and Jackson, D.A. 2001. How well do multivariate data sets match? The advantages of a Procrustean superimposition approach over the Mantel test. Oecologia, **129**(2): 169–178.

Ptacnick, R., Diehl, S., and Berger, S. 2003. Performance of sinking and non-sinking phytoplankton taxa in a gradient of mixing depths. Limnol. Oceanogr. **48**(5): 1903–1912.

Reynolds, C.S. 1984*a*. The ecology of freshwater phytoplankton. University Press, Cambridge, UK.

Reynolds, C.S. 1984*b*. Phytoplankton periodicity: the interactions of form, function and environmental variability. Freshw. Biol. **14**: 111–142.

Reynolds, C.S. 1988. Concept of ecological succession applied to seasonal periodicity of freshwater phytoplankton. Int. Ver. Theor. Angew. Limnol. **23**(2): 683–691.

Ricklefs, R., and Miller, G. 1999. Ecology. 4th ed. Freeman, New York.

Rodier, J. 1978. L'analyse de l'eau. Dunod, Paris, France.

Rossum, J.R., and Villaruz, P.A. 1963. Determination of ammonia by the indophenol method. J. Am. Water Works Assoc. **55**: 657–658.

Shannon, C.E. 1948. A mathematical theory of communication. Bell Syst. Tech. J. **27**: 379–423; 623–656.

Sommer, U. 1985. Comparison between steady state and non-steady state competition: experiments with natural phytoplankton. Limnol. Oceanogr. **30**(2): 335–346.

Sommer, U., Gliwicz, Z.M., Lampert, W., and Duncan, A. 1986. The PEG-model of seasonal succession of planktonic events in fresh waters. Arch. Hydrobiol. **106**(4): 433–471.

Talling, J.F. 1957. Photosynthetic characteristics of some freshwater diatoms in relation to underwater radiation. New Phytol. **56**: 29–50.

Wetzel, R.G. 2001. Limnology: lake and river ecosystems. 3rd ed. Academic Press, San Diego, California.

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The relative importance of local, lateral, and longitudinal variables on the development of habitat quality models for a river[1]

Judith Bouchard and Daniel Boisclair

Abstract: Fish habitat quality models (FHQM) developed for rivers consist of relationships between indices of habitat quality and environmental conditions prevailing within sites (local variables). Given the hierarchical structure of these ecosystems, modeling habitat quality over complete rivers may require the inclusion of variables in FHQM that represent the processes operating over a more complete range of spatial scales. The objectives of this study were to quantify the relative importance of local, lateral (characteristics of the shores), and longitudinal (attributes along the upstream–downstream axis of the river) variables on a FHQM developed for parr of Atlantic salmon (*Salmo salar*). Parr densities (an index of habitat quality) and local, lateral, and longitudinal variables were estimated in 32 reaches of 200 m. FHQM were developed using analytical units (AU) of 50, 100, and 200 m (length of AU in the upstream–downstream axis of the river). The structure and the explanatory power of FHQM were affected by the AU size. In the study river, 98% of the explanatory power of FHQM was imputed to the effect of local variables.

Résumé : Les modèles de la qualité des habitats de poissons (MQHP) développés en rivières sont des relations entre des indices de la qualité des habitats et des conditions environnementales qui prévalent à l'intérieur de sites (variables locales). Compte tenu de la structure hiérarchique de ces écosystèmes, la modélisation de la qualité des habitats pour des rivières entières peut demander l'inclusion dans les MQHP de variables qui représentent les processus qui opèrent sur une plus grande gamme d'échelles spatiales. L'objectif de cette étude est de quantifier l'importance relative des variables locales, latérales (caractéristiques des berges) et longitudinales (attributs sur l'axe amont–aval d'une rivière) sur un MQHP développé pour des tacons du saumon atlantique (*Salmo salar*). La densité de tacons (un indice de la qualité des habitats) et les variables locales, latérales et longitudinales ont été estimées dans 32 segments de 200 m. Les MQHP ont été développés avec des unités d'analyse (UA) de 50, 100 et 200 m (longueur dans l'axe amont–aval de la rivière). La structure et la puissance explicative des MQHP sont affectées par la taille des UA. Dans la rivière étudiée, 98 % de la puissance explicative des MQHP est imputée à l'effet des variables locales.

Introduction

The primary objective of fish habitat quality models (FHQM) is to explain spatial variations of fish habitat quality. Once this is achieved, FHQM may be used to identify environmental variables that determine fish habitat quality, to predict the effect of perturbations on fish, and to delineate areas that should be protected for conservation purposes. FHQM generally consist of relationships between indices of habitat quality observed at a series of sites (e.g., fish presence, density, biomass, growth, production) and environmental conditions prevailing at these sites (Randall and Minns 2000; Boisclair 2001; Rosenfeld 2003). The key attributes of the designs used to develop FHQM are the size of the sampling units (the dimensions of the smallest unit over which variables are estimated), the dispersion of the sampling units (the average distance between sampling units), and the size of the study area (the area or the distance covered by the farthest sampling units). These attributes are expected to influence the structure and the predictive power of FHQM (Wiens 1989; Jelinski and Wu 1996; Folt et al. 1998). They also define the dimensions of the smallest site for which a habitat quality value may be assigned by a FHQM (the grain size sensu Dungan et al. 2002) and the boundaries of the area over which a given FHQM may be applied (the spatial extent). These may be taken as the lower and the upper limits, respectively, of the spatial domain of a FHQM.

Biotic communities in rivers are presumed to be shaped by processes that interact within a hierarchical structure (microhabitat < pool–riffle < reach < segment < river < water-

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shed < geologic and (or) climatic region), and all levels of this hierarchy are expected to have the potential to contribute to habitat quality (Frissell et al. 1986; Schlosser and Angermeier 1995; Wang et al. 2006*b*). According to this view, FHQM should incorporate the environmental variables that best represent the processes operating at all levels of the hierarchy. Efforts directed towards model development, however, have focused particularly on two relatively distinct levels of the hierarchical structure of rivers. Microhabitat-based FHQM have been developed using only environmental conditions estimated within sampling units of 10^0–10^2 m^2 (local variables: depth, substrate, velocity, insect drift rate, prey size). Microhabitat-based FHQM have been used mostly to quantify spatial variations of fish density and feeding or growth potential along riffle–pool sequences and reaches of 10^2–10^3 m in the river for which they were developed (Guay et al. 2000; Rosenfeld and Boss 2001; Heggenes and Salveit Svein 2002). In contrast, landscape-based FHQM combined local variables, often averaged over sampling units of 10^2–10^4 m^2, with variables that represent environmental conditions that may differ among watersheds (climate, geology, land use; Hughes et al. 2006). Landscape-based FHQM have been used to model fish occurrence and community assemblages in complete reaches of numerous rivers distributed over geographic areas of 10^8–10^{12} m^2 (Wall et al. 2004; Gido et al. 2006; Wang et al. 2006*a*). The inclusion, in landscape-based FHQM, of a more complete range of environmental variables may be expected to increase the predictive power and the spatial domain of FHQM. Interestingly, both the microhabitat- and the landscape-based FHQM highlight the importance of a better understanding of the processes that operate at an intermediate level of the hierarchical structure of rivers. While few microhabitat-based FHQM have been applied to model variations of habitat quality along segments and complete rivers (10^3–10^5 m; Hughes 1998; Heggenes et al. 2002; Johansen et al. 2005), there are indications that such operations may require a better understanding of the processes occurring at these scales (Porter et al. 2000; Magalhaes et al. 2002; Smith and Kraft 2005). Similarly, studies aimed at developing landscape-based FHQM emphasize the need to better examine the effect of network structures and longitudinal patterns on habitat quality indices within rivers (Benda et al. 2004; Hitt and Angermeier 2006; Torgensen et al. 2006).

Processes that operate at the intermediate level of the hierarchical structure of rivers (segments to complete rivers; 10^3–10^5 m) remain poorly understood (Fausch et al. 2002). This situation has been attributed to the relative ease to gather data from the field to develop microhabitat-based FHQM and data from geographic information systems to develop landscape-based FHQM (Torgensen et al. 2006). The theoretical framework presently available to develop FHQM that may allow scientists to explain variations of habitat quality indices among reaches of specific rivers underlines the potential role of the spatial context of sites (Grossman et al. 1995; Schlosser and Angermeier 1995; Ward et al. 2002). According to this framework, habitat quality at a site may not be determined only by environmental conditions found within these sites (local variables) but also by conditions found on the shores (lateral variables) and along the upstream–downstream axis of a river (longitudinal variables). For instance, it may be hypothesized that habitat quality at a site may be enhanced by the presence of overhanging riparian vegetation that provides fish with supplementary prey such as terrestrial insects and additional cover against predators (Cummins et al. 1984). Similarly, habitat quality at a site may be affected by variables that represent lateral transfer of material (inorganic or organic), such as the composition, the area, and the average slope of the valley side draining to this site or to its vicinity upstream (Gregory et al. 1991; Schlosser 1991; Stanford and Ward 1993). Habitat quality may also be influenced by the presence of a tributary that contributes to habitat heterogeneity and that constitutes an input of prey and a thermal refuge for fish (Erkinaro 1995; Bardonnet and Baglinière 2000; Benda et al. 2004). The spatial proximity of a site to complementary resources (the distance between a site and feeding, refuge, spawning, or overwintering areas) has also been suggested to affect habitat quality at this site (Dunnings et al. 1992; Schlosser 1995; Kocik and Ferreri 1998). While numerous hypotheses have been proposed to explain variations of fish habitat quality among reaches of a river, most remain untested. The objectives of this study were to quantify the absolute and the relative importance of local, lateral, and longitudinal variables on a FHQM developed for a river and thereby test hypotheses about the influence of the spatial context of sites on the spatial variability of an index of habitat quality within a river.

Materials and methods

Sampling area, species for study, and strategy

The study was conducted in the main branch of the Sainte-Marguerite River (SMR) in the Saguenay region of Quebec (Fig. 1). The main branch of the SMR has two major tributaries: the northwest (42 km from the river mouth) and the northeast (6 km from the river mouth) branches. Mean annual peak daily discharge and mean summer daily discharge at the gauging station located 43 km from the river mouth (FRM) are, respectively, 70 and 3.6 m^3·s^{-1} (Davey and Lapointe 2007). The discharge from the three branches renders this river wadeable over most of its length during summer flows (maximum wetted width of 80 m; maximum depth of 2 m). The SMR consists of a succession of sedimentary links caused by inputs of coarse substrate from glacial deposits and dry lateral sources (Davey and Lapointe 2007). Typical pool–riffle sequences are superimposed on the succession of sedimentary links. Meanders are particularly developed 13 to 23 km and 41 to 52 km FRM. Features such as cascades (85 km FRM) and rapids (40 km FRM) are also present. The SMR was perturbed by the rectification of meanders (41 to 52 km FRM) during the construction of a highway in 1966. Consequently, embankments were made to stabilize the shores. However, except for this highway, the watershed of the SMR is relatively free of anthropogenic perturbation.

Many fish species are present in the main branch of the SMR: Atlantic salmon (*Salmo salar*), brook trout (*Salvelinus fontinalis*), eastern blacknose dace (*Rhinichthys atratulus*), longnose dace (*Rhinichthys cataractae*), longnose sucker (*Catostomus catostomus*), sea lamprey (*Petromyzon marinus*), American eel (*Anguilla rostrata*), and fallfish (*Semotilus corporalis*). However, this study focussed on parr

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Fig. 1. Map of the watershed of the Sainte-Marguerite River (Quebec, Canada). Reaches sampled during the present study are represented by stars.

of Atlantic salmon (1+ and 2+ indiscriminately), because they are ubiquitous in SMR.

Numerous indices of fish habitat quality may be employed when developing FHQM, and whether some are more ecologically meaningful than others is debatable (Rosenfeld 2003). In the present study, we adopted the position expressed by Boisclair (2001) that all indices (e.g., presence or absence, density, biomass, feeding rate, growth rate) contain complementary information and that, as such, they all contribute to a better understanding of the determinants of fish habitat quality. Parr density (number·m^{-2}) was selected as an index of habitat quality, because this variable is relatively simple to estimate and because if fish distribute themselves according to an ideal free distribution (Grant and Imre 2005), fish density at a given site may represent an index of parr productivity (similar growth everywhere × fish density) at this site.

The sampling area (SMR) and the fish selected for study (parr of Atlantic salmon) offer a unique opportunity to test hypotheses regarding the potential effect of the spatial context of sites on habitat quality indices (Table 1). The testing of such hypotheses requires a careful assessment of the methods that should be used to estimate the index of habitat quality and knowledge of the geographic position of many features of a river. Over the past few years, numerous studies have been performed to determine the most efficient method to assess parr density specifically in the SMR (Imre and Boisclair 2004, 2005; Bédard et al. 2005). Other studies permitted the location of many features of the SMR such as spawning areas (Davey and Lapointe 2007), limits of sedimentary links (Davey and Lapointe 2007), potential overwintering areas (Coulombe-Pontbriand and Lapointe 2004), and tributaries (most not visible using geographic information systems) that are essential to the testing of the hypotheses targeted by the present study.

Spatial and temporal context

Fieldwork was performed in 32 reaches, each measuring 200 m in the upstream–downstream axis of the river (Fig. 1). These reaches were distributed in an 88 km segment of the SMR, limited upstream by a waterfall and downstream by the junction of the Sainte-Marguerite and Saguenay rivers. Each reach was divided in 20 sections of 10 m. This approach allowed us to merge contiguous 10 m sections to form analytical units (AU; units employed during the statistical analysis performed to develop FHQM; Dungan et al. 2002; Brind'Amour and Boisclair 2006) of 50, 100, and 200 m. The size of AU is here defined as the length, in the upstream–downstream axis of the river, of the AU resulting from the merging of a specific number of adjacent sections. This size of AU was judged appropriate because it corresponds to the low range of AU employed to develop landscape-based FHQM (Hughes et al. 2006). In addition, Bouchard (2006) assessed the temporal stability of parr density estimates obtained with AU of 10, 20, 50, 100, and 200 m. This analysis indicated that fish density estimated with AU of 10 or 20 m was associated with coefficients of variation (CV) ranging from 30% to 350% and 30% to 175%, respectively (CV estimated for 10 visits to a same reach for four reaches). However, the average CV obtained

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Table 1. Types of environmental conditions used to explain spatial variations of fish density.

Types of variables	Hypothesized role	Reference
Water depth	Defines the volume available to fish for feeding on insect drift	Hughes and Dill 1990
Flow velocity	Determines insect drift rate (no. of insects·h^{-1}) and the costs of foraging	Fausch 1984
Substrate composition	Determines the importance of the cover for fish against high flows and predators	Morantz et al. 1987
Flow type	Represents a mesohabitat (10^2–10^3 m^2) measure of turbulence and energetic costs of habitat use	Bovee et al. 1998; Enders et al. 2005
Woody debris	Contributes to high insect productivity and constitutes fish refuge against predators	Johnson et al. 2006
Pool	Provides fish refuge against high flows	Poff and Huryn 1998
Midchannel bars – islands	Increases habitat heterogeneity and may affect the structure of fish communities	Benda et al. 2004
Sandy shores or cliff	Causes input of sand, embedded substrate, loss of interstices, loss of refuge, lower feeding efficiency, and lower growth	Bolliet et al. 2005
Embankment	Prevents erosion and protect spawning sites; boulders used to construct the embankment may provide fish refuge against high flows and predators	Opperman et al. 2005; Wankowski and Thorpe 1979
Tributary confluence	Provides a thermal refuge and a complementary source of food from insect drift	Bruns et al. 1984; Erkinaro 1995
Overhanging vegetation	Represents an additional source of prey (terrestrial insects) and cover against predators	Cummins et al. 1984
Area and slope of valley side	Contributes to a local input of cool ground water (thermal refuge), organic (food), and inorganic (cover) debris	Gregory et al. 1991; Stanford and Ward 1993
Distance to the river mouth	Represents the global effect of environmental changes expected to occur along a river continuum concept	Vannote et al. 1980; Naiman et al. 1987
Distance to a tributary	Defines the proximity to complementary resources such as thermal refuge or alternate food source	Bruns et al. 1984; Dunnings et al. 1992
Distance to a spawning site	Represents the difficulty (and potential mortality) for fish moving from sites of emergence to other habitats	Kocik and Ferreri 1998
Distance to upstream limits of sedimentary links	Represents the distance to reaches that have high insect productivity and that are good overwintering habitats	Rice et al. 2001; Coulombe-Pontbriand and Lapointe 2004

with AU of 50, 100, and 200 m decreased to 50%, 40%, and 30%, respectively. Because it was logistically impossible, in the present study, to sample 32 reaches of 200 m many times during the short period of the summer when the environmental conditions are relatively stable, parr density in each section was estimated only once; however, we develop FHQM only with AU that minimized the temporal variation of parr density (50, 100, and 200 m). Sampling was conducted between 27 June and 5 August 2003, a period during which parrs are expected to be using summer feeding sites. During this period, water temperature and discharge ranged from 11 to 24.5 °C (average = 17.2 °C; standard deviation = 2.9 °C) and from 2.5 to 23 m^3·s^{-1}, respectively. However, sampling was done when discharge ranged from 2.5 to 4.5 m^3·s^{-1} to minimize the effect of flow variation on our data.

Densities of parr of Atlantic salmon

Parr density in each section was estimated by two observers who simultaneously snorkelled two 10 m long transects oriented approximately parallel to shore. Parr densities were estimated during the night (2200–0300) by underwater observations. The two transects were therefore positioned relative to features of the river that could be easily identified by snorkellers at night (the shores) and that allowed the estimation of fish density over a wide range of environmental conditions within each section. One transect was located as close as possible to the shore (minimum depth of 25 cm), and another was located in the middle of the river (5–40 m from shore depending on river width). We recognize that visual observations performed while snorkelling, like many other methods, provides only a relative index of fish density. Although the SMR is wadeable during average summer flows, snorkelling is the only method that can be applied everywhere and over the complete range of environmental conditions found in this river (Table 2). Hence, estimates of fish density obtained by snorkelling could not be calibrated with other methods because of the difficulty, for instance, to efficiently operate electrofishing gears in 1 m of water with flows of 0.7–0.8 m·s^{-1}. Visual observations were done at night because previous studies performed in the SMR indicated that even in the summer, many parrs remain in the interstices of the substrate during the days and that parr density at night is higher than during daylight hours (Imre and Boisclair 2004; Johnston et al. 2004). In contrast with estimates obtained during daylight hours, estimates of parr density obtained in the SMR by snorkelling at night do not vary significantly among nights and are not significantly affected by the moon phase or the could cover (no sampling was performed when it rained; Girard et al. 2003; Bédard et

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Table 2. Description of dependent and independent variables estimated for analytical units of 50 m.

Variable	Code	Type	Mean	Min.	Max.	CV (%)
Dependent						
Atlantic salmon parr density (parr·m^{-2})	Density	Continuous	0.078	0.000	0.340	89
Independent						
Local						
Clay composition (%) (B axis: ≤0.004 mm)	Clay	Continuous	1	0	33	398
Silt composition (%) (B axis: 0.004–0.06 mm)	Silt	Continuous	1	0	12	220
Sand composition (%) (B axis: 0.06–32 mm)	Sand	Continuous	14	0	86	130
Gravel composition (%) (B axis: 2–32 mm)	Gravel	Continuous	29	0	92	71
Pebble composition (%) (B axis: 32–64 mm)	Pebble	Continuous	19	0	48	65
Cobble composition (%) (B axis: 64–250 mm)	Cobble	Continuous	22	0	61	74
Boulder composition (%) (B axis: 250–1000 mm)	Boulder	Continuous	12	0	58	147
Metric boulder composition (%) (B axis: >1000 mm)	MetricB	Continuous	1	0	13	258
Water depth (m)	Depth	Continuous	0.47	0.22	0.96	35
Flow velocity (m·s^{-1})	Velocity	Continuous	0.40	0.07	0.73	40
Smooth water surface occurrence (%)	SWS	Continuous	93	0	100	19
Rough water surface occurrence (%)	RWS	Continuous	22	0	100	167
Woody debris presence	WoodD	Binary	0.65	0	1	—
Pool presence	Pool	Binary	0.11	0	1	—
Island or midchannel bar presence	Island	Binary	0.23	0	1	—
Lateral						
Area of the region drained on shores of AU (km^2)	AD_AU	Continuous	4	0	471	1095
Averaged slope of the AD_AU (°)	SD_AU	Continuous	10	0.4	26	70
Area of the region drained on shores 500 m upstream AU (km^2)	AD_500m	Continuous	5	0.1	472	865
Averaged slope of the AD_500m (°)	SD_500m	Continuous	15	4	23	26
Area of the region drained on shores 1 km upstream AU (km^2)	AD_1km	Continuous	8	0.5	472	508
Averaged slope of the AD_1km (°)	SD_1km	Continuous	14	8	21	19
Overhanging vegetation	Overveg	Binary	0.73	0	1	—
Sandy shore or cliff	Ssand	Binary	0.52	0	1	—
Embankment	Embank	Binary	0.05	0	1	—
Tributary confluence	Trib	Binary	0.07	0	1	—
Longitudinal						
Distance from the river mouth (m)	Dmouth	Continuous	42 465	3056	85 739	55
Distance to the nearest tributary downstream (m)	DtribD	Continuous	309	0	1 714	117
Distance to the nearest tributary upstream (m)	DtribU	Continuous	439	0	2 790	132
Distance to the nearest tributary (m)	Dtrib	Continuous	177	0	1 300	129
Distance to the nearest spawning site (m)	Dspawn	Continuous	1 917	0	7 820	101
Distance to the nearest upstream limit of a sedimentary link downstream (m)	DlinkD	Continuous	9 791	0	28 748	89
Distance to the nearest upstream limit of a sedimentary link upstream (m)	DlinkU	Continuous	7 631	0	29 353	97
Distance to the nearest upstream of a sedimentary link (m)	Dlink	Continuous	4 062	0	14 586	97

Note: Sample size for all variables is 128 (four analytical units of 50 m per 200 m reach × 32 reaches). CV is the coefficient of variation corrected for small samples (Sokal and Rohlf 1995).

al. 2005; Imre and Boisclair 2005). In summary, snorkelling at night was employed because it could be used everywhere in the SMR, it eliminated the problem of having to deal with different biases inherent to different sampling methods, and it provided estimates that are relative but reliable.

Parr were observed using underwater lighting systems (Underwater Kinetics Light, model C4). Light was directed in an upward direction at an angle of approximately 45° relative to water surface. Hence, fish were illuminated using a diffused beam of light, which is expected to minimize fish disturbance (Gries et al. 1997). For each 10 m section, the two snorkellers swam against the flow and counted the number of parr observed and evaluated the mean visibility. The mean visibility was the average distance (m) at which parr could be seen and correctly identified either on the left or the right of the snorkellers. Parr density (parr·m^{-2}) in a specific transect (shore or middle) of any given 10 m section was obtained by dividing the number of parr observed by the surface area sampled in that transect (mean visibility × two sides × 10 m). Average parr density in any AU was obtained by averaging parr densities of transects within this unit.

Sampling and computation of physical variables

Variations of parr densities were modeled using three categories of physical variables: local, lateral, and longitudinal variables. These physical variables, sampled to explain spa-

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tial variations of fish density, were selected because of their anticipated role as determinants of habitat quality in rivers (see Table 1 for the hypothesized role of each type of physical variable). Local variables described the conditions observed within AU. Local variables were estimated during daylight hours a maximum of 3 days before or after parr densities were estimated at a site (water discharge varied by less than 0.8 $m^3 \cdot s^{-1}$, or 21% of average flow, over this interval). Estimation of the local environmental conditions during daylight hours permitted the identification of all key features of the river, and hence, the assessment of local variables at the three locations presumed to represent the complete range of environmental conditions found in each section. These locations corresponded approximately to the thalweg (part of the cross section of the river where depth and flow rate are highest), the shore farthest from the thalweg (minimum depth of 25 cm), and a point in the middle in these two locations. When no distinct thalweg could be perceived, this location was replaced by the middle of the river. Consequently, local variables were estimated over a more complete range of environmental conditions than parr density. For each 10 m section, we took three estimates of water depth (measuring rod graduated 5 cm), flow velocity (Gurley–Price current meter held at 40% of the water column), substrate composition (visual evaluation within an area of 1.5 m^2 area as percent contribution of eight size classes of substrate determined by their median axis, also known as their B axis; Table 2), and flow type present within the section (smooth water surface: flat water surface or presence of waves up to 3 cm without air bubbles; and rough water surface: uneven water surface with waves ranging from 5 to 10 cm and air bubbles). The average depth, velocity, and substrate composition were calculated for each AU. Smooth water surface and rough water surface were transformed to assess the presence (1) or the absence (0) of these types of flows in at least one of the three locations within each 10 m section. Because smooth water surface was almost always present once within every AU, we calculated the percentage of smooth and rough water surface within each AU. In addition, we visually assessed the presence of woody debris (wood debris consisted of wood fragments longer than 30 cm that covered at least 1 m^2 of the riverbed) and pools in each 10 m section. According to Gordon et al. (2004), "a pool is a region of deeper, slower moving water with fine bed materials". In the SMR, a pool was further defined as a depression of the river bed at least 5 m long in the upstream–downstream axis of the river, where average water depth was at least twice that of the surrounding river bed (the depth of pools ranged from 0.5 to 2 m with an average of 1 m). Woody debris, pools, and islands (or midchannel bars) were coded 1 (presence) if they were present in at least one 10 m section of an AU; otherwise they were coded 0 (absence). River features (pool and island or midchannel bar) were coded present in every contiguous 10 m section where they occurred. When these features were larger than 10 m, they were coded present in every section where they occurred.

Lateral variables referred to characteristics of the shores. The presence of sandy shore or cliff, embankment, tributary confluence (every tributary seen was considered, no matter its size), or overhanging vegetation (covering at least a surface of 1 m^2 above the water) was visually assessed from the river. Other lateral variables were estimated with GIS software (ArcGIS 8.3, ESRI, Redlands, California) and numerical topographic maps (1:20 000). The area and the average slope of the valley side draining to the river were calculated from a numerical elevation raster (raster resolution: 10 m × 10 m). These variables were estimated three ways: for the valley side area draining to the length of bank (*i*) corresponding to the AU, (*ii*) from the AU and extending 500 m upstream, and (*iii*) from the AU and extending 1 km upstream.

Longitudinal variables described the position of AU relative to features on the upstream–downstream axis of the river (distance to river mouth, tributaries, spawning sites, upstream limits of sedimentary link). River mouth and tributaries were localized on topographic maps (1: 20 000). Spawning sites and boundaries of sedimentary link were localized by Davey and Lapointe (2007). Longitudinal variables were estimated using GIS software in which the river was represented by a line that corresponded to the trajectory of the thalweg. For each AU, we estimated the distance to the nearest feature. In the case of tributaries and upstream limits of sedimentary links, we estimated the distance between an AU and the nearest feature upstream and downstream.

Selection of multiple regression models

FHQM of the SMR were developed using multiple regression analysis. Parr densities were modelled using physical variables from one category (local, lateral, or longitudinal) at a time. Physical variables and their natural logarithm (in the case of continuous variables) were selected with a forward selection procedure. We employed two approaches to eliminate FHQM that did not correctly predict parr densities. First, we tested multiple regression models with unrestricted permutation tests (10 000 permutations of parr density). Permutation tests were employed because estimates of parr density were not normal and could not be normalized (Legendre and Legendre 1998). We eliminated models that were not significant or that included variables that did not significantly contribute to a model at an α level of 0.05. Second, we proceeded to the cross-validation of each significant model to eliminate models that did not correctly predict statistically independent data and to select the model with the highest potential to predict such data. The cross-validation was performed as follows: (1) we randomly split our data into a learning set and a testing set of the same size; (2) we used the learning set to develop a multiple regression model based on the independent variables found to have a significant effect during the analysis of the complete data set; (3) we used the model developed with the learning set to predict parr density of the testing set; (4) we compared the predictions made by the model and the observation of the testing set; (5) we repeated 10 000 times steps 1 to 4. The most common procedure to perform a cross-validation exercise is to make one learning set and one testing set. However, replicating the cross-validation 10 000 times allowed us to get a more complete representation of the statistical population of the results of the cross-validation analysis. We assessed the quality of the predictions (step 4) by calculating the major axis slope (b_{MA}), the major axis intercept (b_0), and the coefficient of determination (r^2) between predictions and observations for each replication of the cross-validation

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(Mesplé et al. 1996). The 95% confidence intervals (CI) of these parameters were estimated by calculating the 2.5 and 97.5 percentiles of the 10 000 values obtained for each parameter in step 5. A model was rejected whenever the 95% CI of its b_{MA} included the value of 0 or excluded the value of 1 or when the 95% CI of b_0 excluded the value of 0. We then selected models with the highest median r^2 value estimated by cross-validation for each combination of AU size (50, 100, and 200 m) and variable category (local, lateral, and longitudinal). The median r^2 of the distribution of r^2 obtained for a model was expected to represent the most probable value of r^2, and the model that had the highest median r^2 was taken as the best model. Hence, nine habitat quality models could be obtained (three AU sizes × three categories of variables). The fraction of parr density variations explained by the multiple regression models was determined by computing the adjusted coefficient of multiple determination (R^2_a; Legendre and Legendre 1998).

We evaluated the relative importance of local, lateral, and longitudinal variables by estimating the fraction of the variation of parr densities explained exclusively or simultaneously by the different categories of physical variables. This was achieved in two steps. First, we developed the model that represented the relationship among parr densities estimated at any given AU size and every local, lateral, and longitudinal variable shown to have a significant effect during the cross-validation analysis performed for that AU size. The three resulting models (one for each AU size) are hereafter referred to as the combined models for a given AU size. Second, we proceeded to a variation partitioning for each combined model (Legendre and Legendre 1998). Variation partitioning separates the exclusive contribution of different categories of variables (in our case local, lateral, and longitudinal variables) to the combined model obtained for each AU size. In addition, it permits the determination of the part of the variation of parr density explained simultaneously by two or three categories of physical variables. We anticipated that some physical variables that had a significant effect on parr densities when habitat quality models for a given AU size were developed independently for each category of physical variables (during the cross-validation analysis) may not have a significant effect in the combined model for this AU size because the part of the variance they explained was included in that of another category of physical variables. This is precisely the kind of information required to attain our objective. Because variation partitioning employs the statistics provided by the multiple regression used to develop the combined models, exclusion of a physical variable from this analysis meant that it would be impossible to identify the interaction between the variance explained by this variable and that explained by other variables. Consequently, every local, lateral, and longitudinal variable shown to have a significant effect during the cross-validation analysis performed for a given AU size (even those that did not significantly contribute to explain variations of parr density in the combined model for this AU size) were included in the combined model for this AU size. This strategy allowed us to obtain a complete representation of the exclusive and the joined contribution of the different categories of physical variables to a combined model. This analysis was complemented by the computation, for each AU size, of a correlation matrix (Pearson's r) describing the relationship among the physical variables.

Results

Parr densities and physical conditions

Parr densities estimated for AU of 50 m ranged from 0.0 to 0.34 parr·m^{-2} (Table 2). For AU of 200 m, parr densities ranged from 0.007 to 0.26 parr·m^{-2}. CVs of parr densities ranged from 89% (AU of 50 m) to 77% (AU of 200 m). Physical conditions (local, lateral, and longitudinal) estimated for different AU sizes varied to different degrees depending on the specific variables within each category of physical conditions (Table 2). Local variables for AU of 50 m had CVs that ranged from 19% (smooth water surface) to 710% (bedrock). Lateral variables for this AU size had the largest range of CVs, with 19% for slope of the drainage region within 1 km upstream of the AU and 1095% for the area of the drainage region at the AU. In contrast, longitudinal variables covered the smallest range of CVs, with 55% for the distance to the river mouth and 129% for the distance to the closest tributary. Local and lateral variables had CVs that decreased by as much as 10-fold as the AU size increased from 50 to 200 m. For instance, CVs of the area of the region drained on the river shores 500 m upstream of the AU decreased from 865% (AU of 50 m) to 85% (AU of 200 m). In contrast, the CVs of longitudinal variables increased by at most 1.5-fold as the AU size increased (e.g., CV of the distance to the first tributary downstream increased from 117% to 170% as AU increased from 50 to 200 m).

Fish habitat quality models and the influence of the size of the AUs

No statistically significant model using local variables was developed for AU of 50 m. Models developed using local variables for other sizes of AU explained a maximum of 50% (100 m) to 65% (200 m) of parr density variations (Table 3). The explanatory power of these models therefore tended to increase as the size of the AU increased. For AU of 100 m, a maximum of three variables were selected: boulder, woody debris, and smooth water surface. However, for AU of 200 m, only two variables significantly contributed to explain variations of parr densities: boulder and woody debris. For all sizes of AU analysed, the first local variable to be selected during the forward stepwise procedure was always boulder. This variable alone explained from 41% (AU of 100 m) to 47% (AU of 200 m) of parr density variations (R^2_a). Other local variables increased the R^2_a of 9% (100 m) to 18% (200 m). Independently of the AU size, parr densities were positively correlated with all local variables selected. The coefficient of ln(Boulder + 1) in the model based on local variables was unaffected by the AU size. However, for the model developed with two independent variables for AU of 100 m, the coefficient of woody debris increased from 0.041 to 0.085 as the AU size increased from 100 to 200 m. Lateral variables did not permit the development of statistically significant models to explain variations of parr density, and this regardless of the size of the AU. No statistically significant model using longitudinal variables was developed for AU of 50 m. For larger AU, models developed using lon-

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Table 3. Habitat quality models selected for the three categories of physical variables and the three different sizes of analytical units.

Category of physical variables	Analytical units size (m)	Models of parr density	R_a^2
Local	50	No model selected	—
	100	0.034·ln(Boulder + 1) + 0.041·WoodD – 0.008	0.46
		0.040·ln(Boulder + 1) + 0.036·WoodD + 0.069·ln(SWS + 1) – 0.32	0.50
	200	0.040·ln(Boulder + 1) + 0.085·WoodD – 0.064	0.65
Lateral	50	No model selected	—
	100	No model selected	—
	200	No model selected	—
Longitudinal	50	No model selected	—
	100	–0.017·ln(DlinkU + 1) + 0.22	0.20
	200	–0.014·ln(DlinkU + 1) + 0.19	0.19

Note: R_a^2 is the adjusted coefficient of determination of the models. Two equations are presented for analytical unit of 100 m under Local to illustrate the potential effect of the number of variables on the explanatory power of the models. See Table 2 for the codes of the variables.

gitudinal variables explained from 19% (200 m) to 20% (100 m) of variations of parr densities (Table 3). As may be anticipated, the size of the AU did not have a marked effect on the explanatory power or structure of the models developed using longitudinal variables because these variables do not vary much with the size of AU. Parr density for AU of 100 and 200 m decreased as the distance between AU and the upstream limit of a sedimentary link (DlinkU) increased. The cross-validation indicated that FHQM based on local variables have an ability to predict independent data ($0.47 < r^2 < 0.64$) that is 2- to 3-fold superior than models based on longitudinal variables ($0.22 < r^2 < 0.24$; Fig. 2). In addition, the median r^2 of models developed using local variables increased as the AU size increased from 100 m (0.47) to 200 m (0.64).

Relative importance of local, lateral, and longitudinal variables

The combined models based on local and longitudinal variables explained 51% (100 m) to 65% (200 m) of the variations of parr density (Fig. 3). Variation partitioning indicated that the variance of parr density explained by the combined model could be divided into three fractions. The first and most important fraction was the part of the variance explained exclusively by local variables. This fraction ranged from 31% (AU of 100 m) to 47% (AU of 200 m). The second fraction was the part of the variance explained exclusively by longitudinal variables. This fraction never explained more than 1% of the variation of parr density (AU of 100 m). The third fraction was explained simultaneously by local and longitudinal variables. The joint effect of these variables on combined FHQM models ranged from 18% (AU of 200 m) to 19% (AU of 100 m).

Discussion

Influence of the size of AUs

Our analyses are consistent with the expectation that the AU size may affect specific attributes of relationships between biological and physical variables (Levin 1992; Bellehumeur and Legendre 1998). However, our results indicate that the influence of the AU size may vary among physical variables within a category. The number of local variables having a significant effect on parr density decreased from three to two as the AU size increased from 100 to 200 m. The nature of the variables that significantly contributed to FHQM was more stable among the sizes of AU than their number. For instance, ln(Boulder + 1) and woody debris both contributed to the FHQM based on local variables using AU of 100 and 200 m. The effect of the AU size on the regression coefficients associated with the variables that significantly contributed to explain variations of parr density also varied among variables within a category. The regression coefficients of a local variable such as ln(Boulder + 1) in the two- and the three-variable model based on AU of 100 m differed at most by 15% from that of the model based on AU of 200 m. In contrast, the regression coefficient of woody debris varied 2.1- to 2.4-fold between models developed using AU of 100 and 200 m. The fraction of parr density variation explained by FHQM (R_a^2) based on local variables increased from 0.50 to 0.65, and the ability to predict independent data during a cross-validation exercise (r^2) increased from 0.47 to 0.64 as the AU size increased from 100 to 200 m.

Our study suggests that FHQM based on local variables are structurally (number, nature, and coefficient of variables) and functionally (explanatory power: R^2 and r^2) sensitive to changes in the AU size. Three hypotheses may be proposed to explain that models based on local variables have a better explanatory power for AU of 200 m than for AU of 100 m. First, it may be hypothesized that the model based on local variables for AU of 200 m have a higher explanatory power than the FHQM developed for AU of 100 m because it comprised fewer variables (two explanatory variables for AU of 200 m instead of three for AU of 100 m). It has been demonstrated that model complexity (the number of independent variables) may induce an "over fit" of the data (Gong 1986) and may increase the prediction error (Mac Nally 2000). However, the R_a^2 (0.46) and r^2 (0.45) of the FHQM based on two local variables using AU of 100 m remained lower than models developed using AU of 200 m. The relative performance of FHQM based on local variables and developed us-

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Fig. 2. Distributions of the major axis slopes (b_{MA}), the intercepts (b_0), and the coefficients of determination (r^2) of the relationships between predicted and observed parr density obtained following the cross-validation of the models developed using local (open) and longitudinal variables (shaded) for analytical units of 100 and 200 m.

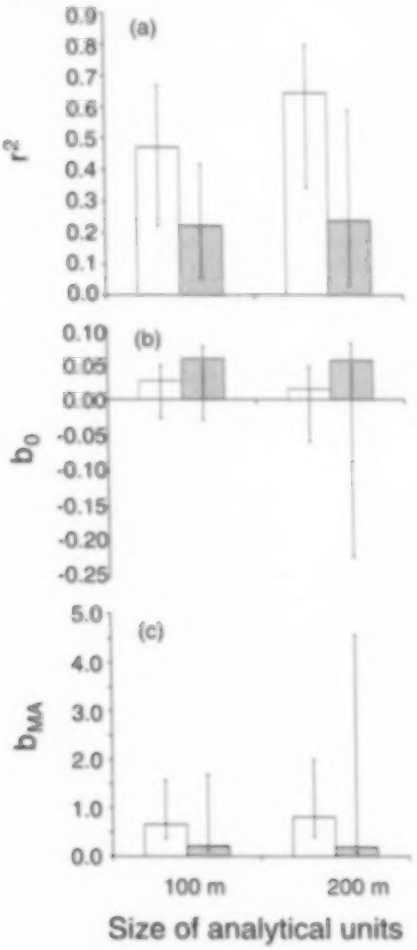
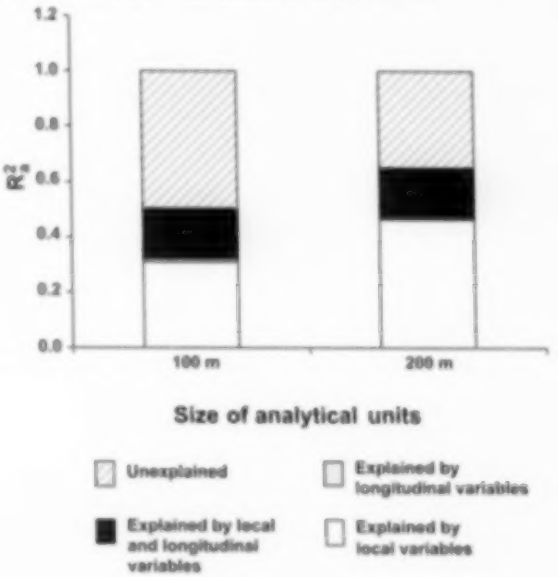


Fig. 3. Explained and unexplained portions of the variance of parr density in combined models developed using analytical units of 100 and 200 m. Explained variance is further divided into portions explained exclusively by local and longitudinal variables and simultaneously by local and longitudinal variables. R_a^2 is the adjusted coefficient of determination of the models.



ing AU of 100 and 200 m may therefore be independent of the number of variables comprised in the models. Second, because sampling for fish and sampling for local environmental conditions was not always performed exactly at the same locations of given 10 m sections, it may be hypothesized that at an AU size of 100 m, parr density was estimated over a sufficiently high range of local environmental conditions for a significant relationship between parr density and local variables to be detected. In any given 10 m section, fish density was estimated near the shore and in the middle of the river. Local environmental conditions were estimated near the shore, in the thalweg (or in the middle of the river when no distinct thalweg could be perceived), and at a location in the middle of these two. This strategy was employed to insure that sampling would characterize the complete range of local environmental condition in any 10 m section. The objective of the sampling was not to identify the structures selected by fish within 10 m sections (as in microhabitat models, e.g., Guay et al. 2000) but among AU ≥ 50 m. Fish density was not estimated in the thalweg or at a location halfway between the shore and the thalweg because, in contrast with the middle of the river, these locations of the river could not always be identified by snorkellers sampling at night. However, the middle of the river (where parr density was estimated) is anticipated to cross the thalweg or the location halfway between the shore and the thalweg (where local conditions were estimated) from time to time. Hence, parr density may have to be estimated over at least 100 m before this variable is estimated in the thalweg (sometimes, but not always, in the middle of the river) or at a location between the thalweg and the shore (sometimes, but not always, in the middle of the river) and before a significant relationship between parr density and local environmental conditions may emerge. Third, it may be hypothesized that the temporal uncertainty related to fish density in individual AU may affect the strength of the relationship between parr density and environmental conditions. In our study, parr density was estimated only once per 200 m reach and in each AU. The effect of the temporal variability of parr density was minimized by developing FHQM with AU ≥ 50 m. However, parr density in AU of 50, 100, and 200 m may vary among nights. Although parr are generally perceived as territorial fish, they are also known to explore their habitats during the summer months (Armstrong et al. 1997; Metcalfe et al. 1997). The possibility that, as suggested by Bouchard (2006), the temporal variability of parr density due to fish movement may decrease with the

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AU size may explain that FHQM based on AU of 200 m may perform better than those based on 100 m and that no statistically significant FHQM could be developed for AU of 50 m. One consequence of the this hypothesis, for which we presently have no support, is that if the movement of fish or the average size of home range of parr changes among rivers, the AU size that should be used to develop FHQM may also vary among rivers.

Relative importance of local, lateral, and longitudinal variables

Variation partitioning demonstrated that local and longitudinal variables shared a lot of information and hence that they are interrelated (Table 4). The fact that local and longitudinal variables shared information supports the suggestion of Rice et al. (2001) that sedimentary links may influence local variables and organisms longitudinal distribution. Parr density was negatively related to DlinkU, which is expected because the percent contribution of boulders to the riverbed is expected to decrease from the upstream to the downstream limit of a sedimentary link. However, DlinkU explained less than 20% of parr density variation, whereas local variables explained 44%–65% of this variation. Consequently, in the SMR, sedimentary links may have contributed to structural local variables but other processes may have played a larger role in determining local variables and, in particular, the percent contribution of boulders to the riverbed.

The spatial context of sites may be hypothesized to affect habitat quality at these sites (Schlosser 1995; Fausch et al. 2002; Wiens 2002). This theoretical framework may be used to formulate a series of hypotheses about the effect of environmental conditions found on the shores of a reach (lateral variables, e.g., indices of the input of inorganic or organic material) and the influence of the spatial proximity of complementary resources along the upstream–downstream axis of a river (longitudinal variables, e.g., tributaries that represent a thermal refuge or upstream limits of sedimentary links that constitute major zones of insect production) on habitat quality at this reach. The present study assessed the influence of 10 lateral variables and 8 longitudinal variables that may be hypothesized to affect habitat quality within a river. Many of these variables represented the distance between a site presumed to be used as a summer foraging area and complementary habitats that may be useful within a few days (thermal refuge, alternate prey source), during other seasons (overwintering habitats), or during other life stages (spawning sites). While many studies have compared the influence of local (e.g., depth, velocity, substrate composition within a reach) and landscape (climate, geology, land use) variables on indices of fish habitat quality (see Hughes et al. 2006), we are not aware of a study that examined such a wide range of variables expected to operate at the intermediate level of the hierarchical structure of rivers (segments to complete rivers; 10^3–10^5 m). However, one difficulty of including such a large number of often correlated, independent variables is to identify which best contributes to explain variations of a dependent variable. This difficulty cannot be solved when developing a sampling design. It is possible to anticipate the existence of a correlation among variables but it is generally impossible to identify a priori which of the variables will explain most of the variations of the dependent variable — this is often the objective of a study. The sampling strategy we employed was to estimate all environmental conditions for which an effect on the spatial variation of parr density could be hypothesized. Identification of the key environmental conditions explaining the variations of parr density was done during the analysis of the data. Variation partitioning was particularly useful in achieving our objective because it is specifically designed to quantify the exclusive and the joined contribution to a model of variables that may be correlated (Legendre and Legendre 1998). This analysis indicated that lateral and longitudinal variables provided very little new information that could be used to explain spatial variations of parr density. In fact, lateral variables never contributed to the FHQM we developed. Variation partitioning indicated that regardless of the AU size employed, at least 98% of the explanatory power of FHQM developed by combining local and longitudinal variables was attributable to the effect of local variables (alone or jointly with longitudinal variable) — a situation that could not be fully appreciated using statistical methods designed to assess the correlation among independent variables (e.g., principal component analysis, correlation matrix; see Table 4). This in turns suggests that the information contained in lateral and longitudinal variables contributed to less than 2% of the variation of parr density explained by FHQM developed in our study, and consequently, that spatial variation of parr density in the SMR is mainly determined by local conditions. We can only presume that sampling parr and local environmental conditions exactly at the same locations of each 10 m section would not modify this interpretation and, if anything, would only increase the perceived effect of the local environmental conditions.

The key interpretation of the present study may be that in the SMR, the summer distribution of parrs is determined by local variables, notwithstanding the spatial context of reaches in this river. However, it would be imprudent to presume that the spatial variation of parr density in other rivers may not be affected by the spatial context of sites. For instance, in a river of a same length and having the same number of tributaries (145), spawning sites (29), and sedimentary links (9), but where these resources are more spatially aggregated, the distance between any given reach potentially used by parr in the summer and these resources would be larger than observed in the present study. It could be predicted, in this case, that parr density should be higher than observed in the present study in a reach where the resources of the river

Table 4. Matrix of correlations among physical variables selected to model parr densities for an analytical unit (AU) of (*i*) 100 m and (*ii*) 200 m.

	WoodD	ln(SWS+1)	ln(DlinkU+1)
AU of 100 m			
ln(Boulder + 1)	–0.39**	–0.55**	–0.48**
WoodD	—	0.32**	0.00
ln(SWS + 1)	—	—	0.30*
AU of 200 m			
ln(Boulder + 1)	–0.48**	—	–0.53**
WoodD	—	—	–0.12

Note: See Table 2 for the codes of the variables. **, $p \leq 0.01$; *, $p \leq 0.5$.

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are concentrated, proximity implying lower losses in terms of population dynamics (high probability of finding the resources = decrease mortality) and bioenergetics (smaller distances = lower energetic costs of using alternate resources). However, parr density should be lower than observed in the present study in a reach farther away from these resources. In this case, the spatial context of a reach may be anticipated to affect fish distribution. The case where the number of resources is changed in a same river length may be trivial (increase resources = increase fish density near these resources), although it must be recognized that adding or eliminating, for instance, a spawning site may not have the same effect everywhere along a river (Kocik and Ferreri 1998). As such, the key challenge of FHQM may not be to identify whether or not any category of variables has an effect on indices of habitat quality but to identify the circumstances under which any given category of environmental conditions expresses, or not, an ecologically significant effect. This perspective is consistent with the divergent results often obtained about the absolute and the relative influence of local and landscape variables on habitat quality indices for invertebrates and fish (Lammert and Allan 1999; Dovciak and Perry 2002; Hughes et al. 2006). It is impossible to identify whether these divergent results arise from the use of different indices of habitat quality, species, life stages, river network structures, seasons, land uses, or climates. Only the study of a wide range of combinations of these conditions will allow scientists to derive general tendencies about the relative importance of local, lateral, and longitudinal variables on habitat quality. The present study therefore contributes to set the first boundaries of the circumstances under which variables that refer to the spatial context of sites do not appear to affect the spatial variation of parr density. In the absence of insurmountable obstacles (dams or falls), the spatial pattern of habitat utilization by parr may not be affected by the spatial context of reaches when these reaches are, on average, within 0.2 km from a tributary (maximum 1.3 km), 1.9 km from a spawning site (maximum 7.8 km), and 4.1 km downstream of the upstream limit of a sedimentary link (maximum 14.6 km). These distances are larger than those traditionally employed to define the dispersal capacities of juvenile Atlantic salmon (e.g., 0.4 km upstream of spawning sites, 1 km downstream of spawning sites; Heggenes and Borgstrom 1991; Beall et al. 1994; Kocik and Ferreri 1998), but they are closer to recent data about the movements of these fish (from 208 to 862 m within a 13-day period in the summer and fall; Økland et al. 2004). Hence, the boundaries identified by the present study, together with studies performed in rivers characterized by different spatial contexts, may contribute to better identify the circumstances that determine the interaction that may exist among the explanatory power of local, lateral, and longitudinal variables on the spatial variations of parr density.

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References

Armstrong, J.D., Braithwaite, V.A., and Huntingford, F.A. 1997. Spatial strategies of wild Atlantic salmon parr: exploration and settlement in unfamiliar areas. J. Anim. Ecol. **66**: 203–211.

Bardonnet, A., and Baglinière, J.-L. 2000. Freshwater habitat of Atlantic salmon (*Salmo salar*). Can. J. Fish. Aquat. Sci. **57**: 497–506.

Beall, E., Dumas, J., Claireaux, D., Barrière, L., and Marty, C. 1994. Dispersal patterns and survival of Atlantic salmon (*Salmo salar* L.) juveniles in a nursery stream. ICES J. Mar. Sci. **51**: 1–9.

Bédard, M.-E., Imre, I., and Boisclair, D. 2005. Nocturnal density patterns of Atlantic salmon parr in the Sainte-Marguerite River, Québec, relative to the time of night. J. Fish Biol. **66**: 1483–1488.

Bellehumeur, C., and Legendre, P. 1998. Multiscale sources of variation in ecological variables: modeling spatial dispersion, elaborating sampling designs. Landsc. Ecol. **13**(1): 15–25.

Benda, L., Poff, N.L., Miller, D., Dunne, T., Reeves, G., Pess, G., and Pollock, M. 2004. The network dynamics hypothesis: how channel networks structure riverine habitats. Bioscience, **54**: 413–427.

Boisclair, D. 2001. Fish habitat modeling: from conceptual framework to functional tools. Can. J. Fish. Aquat. Sci. **58**: 1–9.

Bolliet, V., Bardonnet, A., Jarry, M., Vignes, J.C., and Gaudin, P. 2005. Does embeddedness affect growth performance in juvenile salmonids? An experimental study in brown trout, *Salmo trutta* L. Ecol. Freshw. Fish, **14**: 289–295.

Bouchard, J. 2006. Modélisation de la qualité d'habitat estival des juvéniles de saumons atlantiques (*Salmo salar*) à l'échelle d'une rivière. Mémoire de Maîtrise. Université de Montréal, Département de Sciences Biologiques, Montréal, Qc.

Bovee, K.D., Lamb, B.L., Bartholow, J.M., Stalnaker, C.B., Taylor, J., and Henriksen, J. 1998. Stream habitat analysis using the instream flow incremental methodology. US Geological Survey, Biological Resources Division Information and Technology Report USGS/BRD-1998-0004.

Brind'Amour, A., and Boisclair, D. 2006. Effect of the spatial arrangement of habitat patches on the development of fish habitat models in the littoral zone of a Canadian Shield lake. Can. J. Fish. Aquat. Sci. **63**: 737–753.

Bruns, D.A., Minshall, G.W., Cushing, C.E., Cummins, K.W., Brock, J.T., and Vannote, R.L. 1984. Tributaries as modifiers of the river continuum concept: analysis by polar ordination and regression models. Arch. Hydrobiol. **99**: 208–220.

Coulombe-Pontbriand, M., and Lapointe, M. 2004. Landscape controls on boulder-rich, winter habitat availability and their effects on Atlantic salmon (*Salmo salar*) parr abundance in two fifth-order mountain streams. Can J. Fish. Aquat. Sci. **61**: 648–658.

Cummins, K.W., Minshall, G.W., Sedell, J.R., Cushing, C.E., and Petersen, R.C. 1984. Stream ecosystem theory. Verh. Int. Verein. Limnol. **22**: 1818–1827.

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Davey, C., and Lapointe, M. 2007. Sedimentary links and the spatial organization of Atlantic salmon (*Salmo salar*) spawning habitat in a Canadian Shield river. Geomorphology, **83**: 82–96.

Dinetiak, A.L., and Perry, J.A. 2002. In search of effective scales for stream management: Does agroecoregion, watershed, or their intersection best explain the variance in stream macroinvertebrate communities? Environ. Manag. **30**: 365–377.

Dungan, J.L., Perry, J.N., Dale, M.R.T., Legendre, P., Citron-Pousty, S., Fortin, M.J., Jakomulska, A., Miriti, M., and Rosenberg, M.S. 2002. A balanced view of scale in spatial statistical analysis. Ecography, **25**: 626–640.

Dunnings, J.B., Danielson, J.B., and Pulliam, H.R. 1992. Ecological processes that affect populations in complex landscapes. Oikos, **65**: 169–175.

Enders, E.C., Buffin-Bélanger, T., Boisclair, D., and Roy, A.G. 2005. A model of total swimming costs in turbulent flow for juvenile Atlantic salmon (*Salmo salar*). Can. J. Fish. Aquat. Sci. **62**: 1079–1089.

Erkinaro, J. 1995. The age structure and distribution of Atlantic salmon parr, *Salmo salar* L., in small tributaries and main stems of the subarctic River Teno, northern Finland. Ecol. Freshw. Fish, **4**: 53–61.

Fausch, K.D. 1984. Profitable stream positions for salmonids: relating specific growth rate to net energy gain. Can. J. Zool. **62**: 441–451.

Fausch, K.D., Torgersen, C.E., Baxter, C.V., and Hiram, W.L. 2002. Landscapes to riverscapes: bridging the gap between research and conservation of stream fishes. Bioscience, **52**(6): 483–498.

Folt, C.L., Nislow, K.H., and Power, M.E. 1998. Implications of temporal and spatial scale for Atlantic salmon (*Salmo salar*) research. Can. J. Fish. Aquat. Sci. **55**(Suppl. 1): 9–21.

Frissell, C.A., Liss, W.J., Warren, C.E., and Hurley, M.D. 1986. A hierarchical framework for stream habitat classification: viewing streams in a watershed context. Environ. Manag. **10**: 199–214.

Gido, K.B., Falke, J.A., Oakes, R.M., and Hase, K.J. 2006. Fish-habitat relations across spatial scales in prairie streams. *In* Landscape Influences on Stream Habitats and Biological Assemblages: Proceedings of the Symposium on Influences of Landscape on Stream Habitat and Biological Communities, Madison, Wisconsin, USA, 25–26 August 2004. *Edited by* R.M. Hughes, L. Wang, and P.W. Seelbach. American Fisheries Society, Bethesda, Md. **48**: 265–285.

Girard, P., Boisclair, D., and Leclerc, M. 2003. The effect of cloud cover on the development of habitat quality indices for juvenile Atlantic salmon (*Salmo salar*). Can. J. Fish. Aquat. Sci. **60**: 1386–1397.

Gong, G. 1986. Cross-validation, the jackknife, and the bootstrap: excess error estimation in forward logistic regression. J. Am. Stat. Assoc. **81**: 108–113.

Gordon, N.D., McMahon, T.A., Finlayson, B.L., Gippel, C.J., and Nathan, R.J. 2004. Stream hydrology: an introduction for ecologists. 2nd ed. John Wiley & Sons, Chichester, UK.

Grant, J.W.A., and Imre, I. 2005. Patterns of density-dependent growth in juvenile stream-dwelling salmonids. J. Fish Biol. **67**(Suppl. B): 100–110.

Gregory, S.V., Swanson, F.J., McKee, W.A., and Cummins, K.W. 1991. An ecosystem perspective of riparian zones. Bioscience, **41**: 540–551.

Gries, G., Whalen, K.G., Juanes, F., and Parrish, D.L. 1997. Nocturnal activity of juvenile Atlantic salmon (*Salmo salar*) in late summer: evidence of diel activity partitioning. Can. J. Fish. Aquat. Sci. **54**: 1408–1413.

Grossman, G.D., Hill, J., and Petty, J.T. 1995. Observations on habitat structure, population regulation, habitat use with respect to evolutionary significant units: a landscape perspective for lotic systems. Trans. Am. Fish. Soc. **17**: 381–391.

Guay, J.C., Boisclair, D., Rioux, D., Leclerc, M., Lapointe, M., and Legendre, P. 2000. Development and validation of numerical habitat models for juveniles of Atlantic salmon (*Salmo salar*). Can. J. Fish. Aquat. Sci. **57**: 2065–2075.

Heggenes, J., and Borgstrom, R. 1991. Effect of habitat types on survival, spatial distribution and production of an allopatric cohort of Atlantic salmon *Salmo salar* L., under conditions of low competition. J. Fish Biol. **38**: 267–280.

Heggenes, J., and Saltveit Svein, J. 2002. Effect of aquatic mosses on juvenile fish density and habitat use in the regulated River Suldalslagen, Western Norway. River Res. Appl. **18**: 249–264.

Heggenes, J., Saltveit, S.J., Bird, D., and Grew, R. 2002. Static habitat partitioning and dynamic selection by sympatric young Atlantic salmon and brown trout in south-west England streams. J. Fish Biol. **60**: 72–86.

Hitt, N.P., and Angermeier, P.L. 2006. Effects of adjacent streams on local fish assemblage structure in western Virginia: implications of biomonitoring. *In* Landscape Influences on Stream Habitats and Biological Assemblages: Proceedings of the Symposium on Influences of Landscape on Stream Habitat and Biological Communities, Madison, Wisconsin, USA, 25–26 August 2004. *Edited by* R.M. Hughes, L. Wang, and P.W. Seelbach. American Fisheries Society, Bethesda, Md. **48**: 75–86.

Hughes, N.F. 1998. A model of habitat selection by drift feeding stream salmonids at different scales. Ecology, **79**: 281–294.

Hughes, N.F., and Dill, L.M. 1990. Position choice by drift-feeding salmonids: model and test for Arctic grayling (*Thymallus arcticus*) in subarctic mountain streams, interior Alaska. Can. J. Fish. Aquat. Sci. **47**: 2039–2048.

Hughes, R.M., Wang, L., and Seelbach, P.W. (*Editors*). 2006. Landscape Influences on Stream Habitats and Biological Assemblages: Proceedings of the Symposium on Influences of Landscape on Stream Habitat and Biological Communities, Madison, Wisconsin, USA, 25–26 August 2004. Symposium 48. American Fisheries Society, Bethesda, Md.

Imre, I., and Boisclair, D. 2004. Age effects on diel activity patterns of juvenile Atlantic salmon: parr are more nocturnal than young-of-the-year. J. Fish Biol. **64**: 1731–1736.

Imre, I., and Boisclair, D. 2005. Moon phase and nocturnal density of Atlantic salmon parr in the Sainte-Marguerite River, Québec. J. Fish Biol. **66**: 198–207.

Jelinski, D.E., and Wu, J. 1996. The modifiable areal unit problem and implications for landscape ecology. Landsc. Ecol. **11**: 129–140.

Johansen, M., Elliott, J.M., and Klemetsen, A. 2005. A comparative study of juvenile salmon density in 20 streams throughout a very large river system in northern Norway. Ecol. Freshw. Fish, **14**: 96–110.

Johnson, L.B., Host, G.E., and, Olker, J.H. 2006. Landscape- and reach-scale predictors of large wood abundance in low-gradient streams. *In* Landscape Influences on Stream Habitats and Biological Assemblages: Proceedings of the Symposium on Influences of Landscape on Stream Habitat and Biological Communities, Madison, Wisconsin, USA, 25–26 August 2004. *Edited by* R.M. Hughes, L. Wang, and P.W. Seelbach. American Fisheries Society, Bethesda, Md. **48**: 151–173.

Johnston, P., Bergeron, N.E., and Dodson, J.J. 2004. Diel activity patterns of juvenile Atlantic salmon in rivers with summer water temperature near the temperature-dependent suppression of diurnal activity. J. Fish Biol. **65**: 1305–1318.

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Kocik, J.F., and Ferreri, P.C. 1998. Juvenile production variation in salmonids: population dynamics, habitat, and the role of spatial relationships. Can. J. Fish. Aquat. Sci. **55**(Suppl. 1): 191–200.

Lammert, M., and Allan, J.D. 1999. Assessing biotic integrity of streams: effects of scale in measuring the influence of land use/cover and habitat structure on fish and macroinvertebrates. Environ. Manag. **23**: 257–270.

Legendre, P., and Legendre, L. 1998. Numerical ecology. Elsevier, Amsterdam, The Netherlands.

Levin, S.A. 1992. The problem of pattern and scale in ecology. Ecology, **73**(6): 1943–1967.

Mac Nally, R. 2000. Regression and model-building in conservation biology, biogeography and ecology: the distinction between — and reconciliation of — 'predictive' and 'explanatory' models. Biodivers. Conserv. **9**: 655–671.

Magalhaes, M.F., Batalha Diogo, C., and Collares-Pereira, M.J. 2002. Gradients in stream fish assemblages across a Mediterranean landscape: contributions of environmental factors and spatial structure. Freshw. Biol. **47**: 1015–1031.

Mesplé, F., Troussellier, M., Casellas, C., and Legendre, P. 1996. Evaluation of simple statistical criteria to qualify a simulation. Ecol. Model. **88**: 9–18.

Metcalfe, N.B., Valdimarsson, S.K., and Fraser, N.H.C. 1997. Habitat profitability and choice in a sit-and-wait predator: juvenile salmon prefer slower currents on darker nights. J. Anim. Ecol. **66**: 866–875.

Morantz, D.L., Sweeney, R.K., Shrivell, C.S., and Longard, D.A. 1987. Selection of microhabitat in summer by juvenile Atlantic salmon (*Salmo salar*). Can. J. Fish. Aquat. Sci. **44**: 120–129.

Naiman, R.J., Melillo, J.M., Lock, M.A., and Ford, T.E. 1987. Longitudinal patterns of ecosystem processes and community structure in a subarctic river continuum. Ecology, **68**: 1139–1156.

Økland, F., Thorstad, E.B., and Naesje, T.F. 2004. Is Atlantic salmon production limited by number of territories? J. Fish Biol. **65**: 1047–1055.

Opperman, J.J., Lohse, K.A., Brooks, C., Kelly, N.M., and Merenlender, A.M. 2005. Influence of land use on fine sediments in salmonid spawning gravels within the Russian River Basin, California. Can. J. Fish. Aquat. Sci. **62**: 2740–2751.

Poff, N.L., and Huryn, A.D. 1998. Multi-scale determinants of secondary production in Atlantic salmon (*Salmo salar*) streams. Can. J. Fish. Aquat. Sci. **55**(Suppl. 1): 201–217.

Porter, M.S., Rosenfeld, J., and Parkinson, E.A. 2000. Predictive models of fish species distribution in the Blackwater drainage, British Columbia. N. Am. J. Fish. Manag. **20**: 349–359.

Randall, R.G., and Minns, K.C. 2000. Use of fish production per unit biomass ratios for measuring the production capacity of fish habitats. Can. J. Fish. Aquat. Sci. **57**: 1657–1667.

Rice, S.P., Greenwood, M.T., and Joyce, C.B. 2001. Tributaries, sediment sources, and the longitudinal organisation of macroinvertebrate fauna along river systems. Can. J. Fish. Aquat. Sci. **58**: 824–840.

Rosenfeld, J.S. 2003. Assessing the habitat requirements of stream fishes: an overview and evaluation of different approaches. Trans. Am. Fish. Soc. **132**: 953–968.

Rosenfeld, J.S., and Boss, S. 2001. Fitness consequences of habitat use for juvenile cutthroat trout: energetic costs and benefits in pool and riffles. Can. J. Fish. Aquat. Sci. **58**: 585–593.

Schlosser, I.J. 1991. Stream fish ecology: a landscape perspective. Bioscience, **41**: 704–712.

Schlosser, I.J. 1995. Critical attributes that influence fish population dynamics in headwater streams. Hydrobiologia, **303**: 71–81.

Schlosser, I.J., and Angermeier, P.L. 1995. Spatial variation in demographic processes of lotic fishes: conceptual models empirical evidence, and implications for conservation. *In* Proceedings of the Symposium on Evolution and the Aquatic Ecosystem: Defining Unique Units in Population Conservation, Monterey, California, USA, 23–25 May 1994. *Edited by* J. Nielsen. American Fisheries Society, Bethesda, Md. **17**: 392–401.

Smith, T.A., and Kraft, C.E. 2005. Stream fish assemblages in relation to landscape position and local habitat variables. Trans. Am. Fish. Soc. **134**: 430–440.

Sokal, R.R., and Rohlf, F.J. 1995. Biometry. W.H. Freeman and Company, New York.

Stanford, J.A., and Ward, J.V. 1993. An ecosystem perspective of alluvial rivers: connectivity and the hyporheic corridor. J. North Am. Benthol. Soc. **12**: 48–60.

Torgensen, C.E., Baxter, C.V., Li, H.W., and McIntosh, B.A. 2006. Landscape influences on longitudinal patterns of river fishes: spatially continuous analysis of fish-habitat relationships. *In* Landscape Influences on Stream Habitats and Biological Assemblages: Proceedings of the Symposium on Influences of Landscape on Stream Habitat and Biological Communities, Madison, Wisconsin, USA, 25–26 August 2004. *Edited by* R.M. Hughes, L. Wang, and P.W. Seelbach. American Fisheries Society, Bethesda, Md. **48**: 473–492.

Vannote, R.L., Minshall, G.W., Cummins, K.W., Sedell, J.R., and Cushing, C.E. 1980. The river continuum concept. Can. J. Fish. Aquat. Sci. **37**: 130–137.

Wall, S.S., Berry, C.R., Jr., Blausey, C.M., Jenks, J.A., and Kopplin, C.J. 2004. Fish-habitat modelling for gap analysis to conserve the endangered Topeka shiner (*Notropis topeka*). Can. J. Fish. Aquat. Sci. **61**: 954–973.

Wang, L., Seelbach, P.W., and Lyons, J. 2006*a*. Effects of levels of human disturbance on the influence of catchment, riparian, and reach-scale factors on fish assemblages. *In* Landscape Influences on Stream Habitats and Biological Assemblages: Proceedings of the Symposium on Influences of Landscape on Stream Habitat and Biological Communities, Madison, Wisconsin, USA, 25–26 August 2004. *Edited by* R.M. Hughes, L. Wang, and P.W. Seelbach. American Fisheries Society, Bethesda, Md. **48**: 199–219.

Wang, L., Seelbach, P.W., and Hughes, R.M. 2006*b*. Introduction to landscape influences on stream habitats and biological assemblages. *In* Landscape Influences on Stream Habitats and Biological Assemblages: Proceedings of the Symposium on Influences of Landscape on Stream Habitat and Biological Communities, Madison, Wisconsin, USA, 25–26 August 2004. *Edited by* R.M. Hughes, L. Wang, and P.W. Seelbach. American Fisheries Society, Bethesda, Md. **48**: 1–24.

Wankowski, J.W.J., and Thorpe, J. E. 1979. Spatial distribution and feeding in Atlantic salmon, *Salmo salar* L., juveniles. J. Fish. Biol. **14**: 239–247.

Ward, J.V., Malard, F., and Tockner, K. 2002. Landscape ecology: a framework for integrating pattern and process in river corridors. Landsc. Ecol. **17**(Suppl. 1): 35–45.

Wiens, J.A. 1989. Spatial scaling in ecology. Funct. Ecol. **3**: 385–397.

Wiens, J.A. 2002. Riverine landscapes: taking landscape ecology into the water. Freshw. Biol. **47**(4): 501–515.

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Dorsal-fin spine growth of *Heterodontus portusjacksoni*: a general model that applies to dorsal-fin spines of chondrichthyans?

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Abstract: A prospective model of dorsal-fin spine growth in chondrichthyans is devised by studying the growth of spines from captive and wild *Heterodontus portusjacksoni* injected with several fluorochromes. Evidence was found for only two dentine layers in the spine trunk of *H. portusjacksoni*, contrasting with conjectures about the presence of a third middle dentine layer in some squalids. The spines have three simultaneous growth zones. The first growth zone is along the internal edge of the inner trunk dentine layer, where growth bands are deposited towards the centre (centripetally), increasing spine length and width by pressure against the cartilage rod. The second growth zone is along the external edge of the outer trunk dentine layer at the spine base, where growth bands are deposited in an opposite direction to the centre (centrifugally), increasing spine width. A third growth zone at the base of the cap enables downward expansion over the trunk. The model of concentric cones describes correctly the inner dentine layer growth pattern, whereas the outer dentine layer growth increments appear to be related to the external bands on the surface of the trunk. Growth increments from the three growth zones of the spine are all potentially useful for age estimation.

Résumé : Nous mettons au point un modèle prospectif de la croissance de l'épine de la nageoire dorsale chez les chondrichtyens en étudiant la croissance de l'épine chez des *Heterodontus portusjacksoni* captifs et sauvages après injection avec plusieurs fluorochromes différents. Nous arrivons à démontrer l'existence de seulement deux couches de dentine dans le tronc de l'épine d'*H. portusjacksoni*, ce qui va à l'encontre de conjectures sur la présence d'une troisième couche intermédiaire de dentine chez certains squalidés. Les épines possèdent trois zones simultanées de croissance. La première zone de croissance se situe le long de la bordure interne de la couche de dentine interne du tronc et les bandes de croissance y sont déposées vers le centre (de manière centripète) augmentant ainsi la longueur et la largeur de l'épine par pression sur la baguette de cartilage. La seconde zone de croissance se trouve à la bordure externe de la couche de dentine externe du tronc à la base de l'épine et les bandes de croissance s'y déposent en direction opposée au centre (de manière centrifuge) accroissant ainsi la largeur de l'épine. Une troisième zone de croissance à la base du chapeau permet l'expansion de celui-ci vers le bas par-dessus le tronc. Le modèle des cônes concentriques décrit avec justesse le patron de croissance de la couche de dentine interne, alors que les incréments de croissance de la couche externe de dentine semblent être reliés aux bandes externes sur la surface du tronc. Les incréments de croissance des trois zones de croissance peuvent tous potentiellement servir à l'estimation de l'âge.

[Traduit par la Rédaction]

Introduction

Chondrichthyan age estimation is mostly achieved by counting the number of growth-increment bands in hard-tissue structures such as calcified vertebrae and dorsal-fin spines. The presence of dorsal-fin spines in some groups of sharks, as well as in holocephalans, is potentially useful for age estimation, but a lack of understanding of the internal

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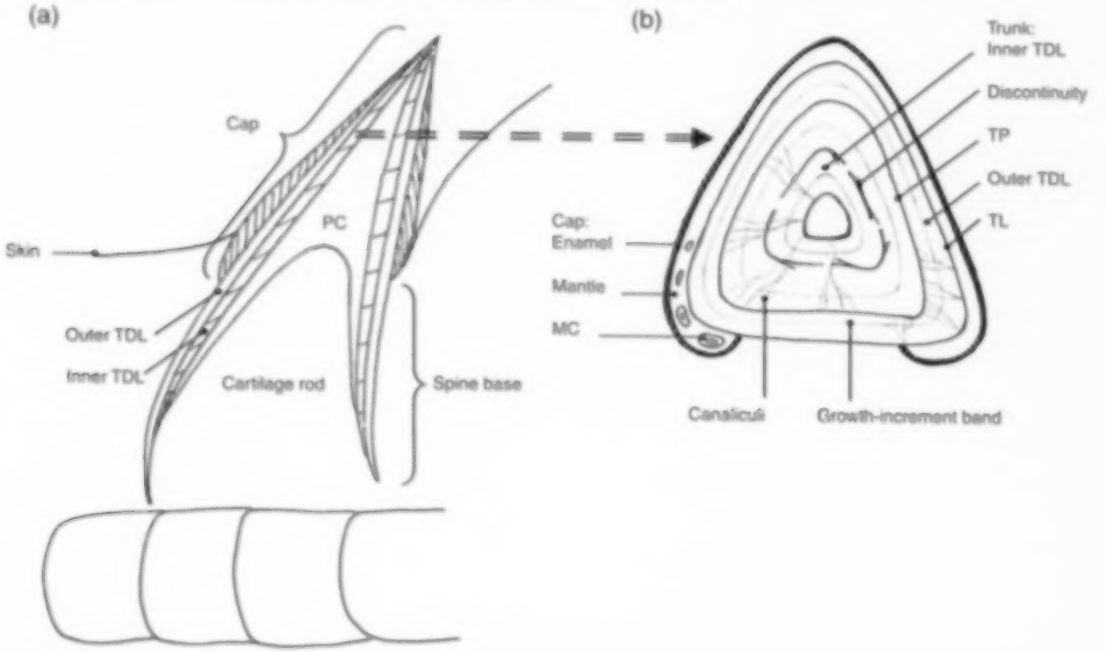
Fig. 1. Diagram of a dorsal-fin spine from *Heterodontus portusjacksoni* (modified from Maisey 1979). Longitudinal section (*a*) and cross section (*b*) at the level of the arrow. PC, pulp cavity; TDL, trunk dentine layer; TP, trunk primordium; TL, transitional layer; MC, mantle canals. Uncertain cartilage rod and pulp cavity height is relative to the TDLs.



structure and growth patterns of dorsal-fin spines has limited their use. Dorsal-fin spines are used for ageing some squalid sharks and holocephalans (Cailliet and Goldman 2004), but their use is not reported for heterodontid sharks.

The indented structure of dorsal-fin spines of chondrichthyans has been described, and its morphogenesis in heterodontid and squalid sharks is similar (Maisey 1979). The spine consists of a cap covering the upper region of the spine, the spine trunk, and an inner pulp cavity above a cartilaginous rod (Fig. 1). The cap comprises an external enamel layer and other associated tissues, such as the mantle. Often confused with the entire cap, the mantle is only a thin dentine layer penetrated by longitudinal vascular canals called mantle canals. The trunk is formed by concentric layers of dentine, each separated by a trunk primordium. The trunk dentine layers (TDLs) are distinct from the dentine layer of the mantle and separated from this by the transitional layer. Odontoblasts on those parts of the external surface of the outer TDL not covered by the cap are involved in the dentine formation (dentinogenesis) of the outer TDL (Maisey 1979).

Ridges on the external surface of the spine cap (enamel bands) are widely used for ageing *Squalus acanthias* and *Squalus megalops* (Holden and Meadows 1962; Beamish and McFarlane 1985; Braccini et al. 2007), but cross sections of spines are used for species where a banding pattern on the cap surface is not evident or distinguishable (Tanaka 1990; Clarke et al. 2002*a*; Calis et al. 2005). More recently, ridges on the surface of the spine trunk, referred as external bands, were used to age *Centroselachus crepidater* (Irvine et al. 2006). These authors agree that the spine trunk is formed by TDLs, but the number of layers and the way they are deposited remain uncertain. Some authors recognize the presence of two TDLs (Maisey 1979; Clarke et al. 2002*a*; Calis et al. 2005), whereas others report a third middle TDL (Beamish and McFarlane 1985; Tanaka 1990; Irvine et al. 2006).

Incorporation of oxytetracycline (OTC) on the spine cap surface, the base of the spine, and the inner TDL of spines of *S. acanthias* suggests an annual growth-increment banding (Beamish and McFarlane 1985). There is no published evidence, however, that the middle and inner TDLs are separated. As pointed out by Clarke et al. (2002*a*), the presence of discontinuities in the inner TDL may have led some authors to interpret part of this layer as a middle TDL. Determining the number of TDLs is essential because of the possibility of under- or over-estimation of age, with potential flow-on effects of biased fishery assessment and misguided management (Summerfelt and Hall 1987; Campana 2001).

To better understand the growth pattern of the dorsal-fin spines of the Port Jackson shark (*Heterodontus portusjacksoni*) and other chondrichthyans, we examined the structure and growth of the spines from captive and wild *H. portusjacksoni* injected with several fluorochromes as hard-tissue dyes. Endemic to southern Australia (Last and Stevens 1994), *H. portusjacksoni* is commonly caught as bycatch by several commercial fisheries (Walker et al. 2005). Age information for this species is required to better understand its population dynamics and the effects of fishing on its populations, so that understanding the growth pattern of dorsal-fin spines is of critical importance.

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Materials and methods

Use of fluorochromes in captive sharks

Five female *H. portusjacksoni* were held captive for 1.5–2.0 years. These specimens were obtained from the commercial catches in Mallacoota, Victoria, and transported in a 1000 L tank with seawater and constant air supply to the laboratories of Primary Industries Research Victoria in Queenscliff, Victoria, Australia. During the first 18 months of the study, they were kept in an outdoor 27 000 L circular tank (~7 m diameter and ~1.5 m deep) with a constant flow of seawater pumped from Port Phillip Bay, Victoria (10 000 $L \cdot h^{-1}$). The temperature of the water in the tank varied seasonally with ambient water temperature in the Bay; average daily water temperatures varied from 11.4 °C during winter to 19.7 °C during summer. The sharks were exposed to normal day and night and normal seasonal light variation. A shade-cloth roof was placed over the tank to reduce sunlight intensity. During the last 9 months of the study, the sharks were transferred to a smaller indoor 5000 L circular tank. Water conditions were similar to those for the earlier part of the study, but artificial light was used to illuminate the tank during daylight hours. The sharks were fed to satiation three times a week, mainly with pilchards. They were occasionally fed live sea urchins, squid, clams, mussels, and prawns.

The sharks were measured, weighed, and injected with fluorochromes every 6 or 12 months, a single fluorochrome being injected at a time. Total length (TL) was measured to the nearest millimetre as a straight line from the tip of the snout to the distal end of the tail while the shark was in a natural position without stretching it. Mass was recorded with a spring balance (±25 g). Three different fluorochrome hard-tissue dyes — OTC (Terramycin/LA, Pfizer), Alizarin Red S (ARS) (Aldrich), and calcein (Sigma-Aldrich) — were used to provide a "date stamp" against which to compare the position of growth-increment bands formed subsequently. These fluorochromes were successfully used in other shark ageing studies and produced fluorescent marks in vertebrae (Officer et al. 1997) and spines (Beamish and McFarlane 1985), persisting as marker of growth for extensive periods of time (Smith et al. 2003). All fluorochromes were used at a concentration of 25 $mg \cdot kg^{-1}$ shark mass, based on experiments on the toxicity of OTC in *H. portusjacksoni* (Walker et al. 1995) and other species (Officer et al. 1997) and on the incorporation time of this fluorochrome in the species (Izzo et al. 2007). Fluorochrome (OTC) marks are visible on the dorsal-fin spines of *H. portusjacksoni* 2 days after treatment; thus, there is no substantial time lag between fluorochrome injection and band formation (Izzo et al. 2007).

Use of fluorochromes in wild sharks

The spines of eight sharks (five males and three females) injected with OTC and released into the wild were analysed after recapture. These sharks were at liberty for periods between 149 and 314 days. All injected wild sharks were caught and tagged during commercial trawling operations and during surveys on board RV *Ngerin* between April 2004 and March 2005 in Spencer Gulf, South Australia. Wild sharks were measured in the same way as captive sharks, weighed, and tagged with rototags (Dalton ID Systems LTD, Oxon, UK). Doses of OTC used for these sharks were similar to those used for captive animals. Tagged specimens were allowed to recover on board in seawater tanks for 30–45 min prior to being released.

Table 1. Excitation and emission wavelengths of the dichroic mirror filters used for the examination of the fluorochromes used.

Fluorochrome	Filter block code	Excitation range (nm)	Emission range (nm)
OTC	D	355–425	>460
Calcein	I3	450–490	>520
ARS	N2.1	515–560	>580

Note: OTC, oxytetracycline; ARS, Alizarin Red S. Filter block code by Leica Instruments P/L, Victoria, Australia.

Tissue collection and processing

Sharks were sacrificed with an overdose of the anaesthetic benzocaine. After sacrifice of the animals, both first and second dorsal-fin spines from all injected sharks (captive and wild) were removed by cutting the spines at their base over the vertebral column. Spines were cleaned with a scalpel and washed with tap water. After cleaning, the spines were air-dried and stored in labelled paper envelopes in a dark, cool place to avoid loss of fluorescence. Longitudinal sections and cross sections of the spines (~300 μm thick) were cut using a lapidary saw (Gemmasta®) after embedding the structures in polyester resin. Cross sections were taken every 2 mm from the tip to the base of the spine. The sections were mounted on glass microscope slides and sealed with cover slips.

Interpretation of growth-increment bands

The dorsal-fin spine terminology used follows Maisey (1979), as this proved to be consistent with the spines external and internal structure, whereas the age- and growth-related terms used generally follow Clarke and Irvine (2006).

The sections were examined and photographed under a compound microscope using ultraviolet (UV) light with an attached camera (Leica DC300F) and a variety of filter blocks appropriate to the fluorochromes used (Officer 1995) (Table 1). The number of growth-increment bands (enamel bands, external bands, and growth-increment bands in the TDLs), discontinuities, and presence and positions of the fluorescent marks in each part of the spines were recorded. A growth-increment band consists of an opaque zone and a translucent zone in the spine TDLs (Cailliet and Goldman 2004) when viewed unstained with transmitted light. Enamel bands comprise ridges on the surface of the spine caps, whereas external bands comprise growth-increment bands on the surface of the trunk (Clarke and Irvine 2006). A discontinuity consists of an abrupt check or band within a TDL traversed by blood vessels (canaliculi) (Clarke et al. 2002*a*). False fluorescent marks produced by autofluorescence of some proteins in the tissues surrounding the structures were distinguished by their colour (OTC appears gold or yellow, whereas autofluorescence appears green or blue under certain UV wavelengths) and by close inspection of the marks at 10× or 25× magnification (Fielder 2002). An ordinal scale of the intensity of the fluorochromes adapted from Logsdon et al. (2004) was used (Table 2). Records were made of whether the fluorescent mark was part of a translucent band

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Table 2. Ordinal scale of the intensity of oxytetracycline marks in calcified structures of elasmobranches (adapted from Logsdon et al. 2004).

Score	Intensity	Definition
0	Absent	No mark present
1	Faint	Mark is present but not clearly visible
2	Visible	Mark is readily visible but not vivid
3	Intense	Mark is both readily visible and vivid

or an opaque band, and the number of growth-increment bands formed after or between the fluorescent marks was counted and compared with the time-at-liberty or time-in-captivity to determine if these bands are formed annually. Three nonconsecutive growth-increment band counts were made for each section, without prior knowledge of the animal's length, sex, or previous counts. The first translucent band was interpreted as the first winter (birth band), as the eggs of the species commonly hatch during winter; the subsequent translucent bands were interpreted as completed years of age.

Comparisons of the number of growth-increment bands and the presence or absence of florescent marks between sex or size groups were not undertaken because of the limited number of specimens for each sex and size. Instead, a general model was developed assuming a similar growth pattern of the dorsal-fin spine in both sexes.

Results

All captive and wild sharks grew in length and mass during the study with the exception of two individuals. A captive shark decreased in mass during the last few months of the experiment, and a wild shark that was shorter at recapture than at release (Table 3). The lengths of sharks analysed for females ranged from 377 to 970 mm TL and the apparent ages from 1 to 18 years; for males, the respective values were from 430 to 660 mm TL and from 3 to 12 years.

The three injected fluorochromes (OTC, ARS, and calcein) were observed under UV light in the dorsal-fin spines of all the captive and wild sharks. The fluorescent marks appeared as a discrete line near the base of the spine cap (Fig. 2) (intensity scores over 2 for all fluorochromes). Evidence of only two TDLs, separated by a conspicuous primordium, was found in the spine trunk. Fluorescent marks appeared as rings near the internal edge of the inner TDL (close to the pulp cavity) (intensity scores over 2 for all fluorochromes) and near the external edge of the outer TDL in cross sections of spines (intensity scores 1–2 for all fluorochromes), but only in sections below the skin and close to the base of the spine (Figs. 3, 4, and 5). Fluorescent marks appeared also as a ring near the internal edge of the mantle canals (Fig. 5*b*) (intensity scores 1–2 for all fluorochromes).

Fluorescent marks in cross sections of the spine showed that the inner TDL grew centripetally towards the pulp cavity (Fig. 3), whereas the fluorescent marks in longitudinal sections showed that these growth-increment bands were deposited along the entire length of the spine where the pulp cavity is open (Fig. 4). In these sections, individual growth increments in the outer TDL could be followed only along some regions of the spine, ending before reaching the tip of the spine or the base of the spine. The upper limit of these outer TDL layers was observed to reach the outer edge of the spine trunk, although the outer TDL layer edges were often not clear. Fluorescent marks were also found around the outer TDL in longitudinal and cross sections only in the region below the skin, close to the base of the spine (Figs. 4 and 5). Fluorescence appeared irregular and patchy along the edge of outer TDL in longitudinal sections, being most distinct at the very base of the spine.

A prominent discontinuity in the inner TDL was observed in some spine sections, but no fluorescent marks were observed around it (intensity score 0 for all fluorochromes), indicating this is not a growth area. Prominent discontinuities were found in sections of dorsal-fin spines of sharks larger than 900 mm TL (samples E4972 and C1998) (Fig. 3*a*), but were absent in smaller specimens. The inner TDL canaliculi originate in the peripheral tissues of the pulp cavity, always crossing all the inner TDLs (including the discontinuity if present) to reach the trunk primordium. The outer TDL canaliculi originate at the transitional layer in the region where the cap is present or at the odontoblast layer below the insertion of the skin, crossing to the trunk primordium in the opposite direction to the inner TDL canaliculi.

Fluorescent marks from fluorochromes injected during winter months were found in the translucent bands, whereas fluorescent marks from fluorochromes injected during summer months were found in the opaque bands.

Discussion

The fluorescent marks found in sectioned spines of *H. portusjacksoni* in this study (i.e., at the base of spine caps, in the inner TDL, and in some parts of the outer TDL) indicate that these structures have three growth zones. The first growth zone is along the internal edge of the inner TDL, where growth bands are deposited towards the centre of the pulp cavity (centripetally), increasing spine width and length by pushing against the cartilage rod (Fig. 6). The second growth zone is at the spine trunk periphery, along the external edge of the outer TDL at the base of the spine, where growth bands are deposited in the opposite direction to the centre (centrifugally), resulting in the formation of the external bands. The third growth zone is at the base of the cap, producing a downward extension of the cap to continuously cover the spine trunk as it grows outwards from the skin. Evidence of fluorescence on spine caps, in the inner TDL, and on the surface of the base of the spine trunk of *Squalus acanthias* (Beamish and McFarlane 1985) suggests that this growth pattern could be similar in the dorsal-fin spines of other chondrichthyan species.

The inner TDL growth pattern is such that new growth-increment bands are not formed in the more distal region of the spine where the pulp cavity has been completely filled. This interpretation is supported by the lack of fluorescent marks in cross sections of the distal region of the spine and by lower counts of growth-increment bands in cross sections of the distal region than counts in cross sections through regions of the spine where the pulp cavity is open (Tovar-Ávila 2006). Because of continuous growth in length and

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Table 3. Fluorescent marker injections in captive and wild sharks.

Sample No.	Sex	Capture Length (mm)	Capture Mass (g)	Date of injection OTC	ARS	Calcein	Period of survival (months)	Sampling Date	Length (mm)	Mass (g)
Captive sharks										
E4972	F	906	7100	25 July 2003	13 July 2004	14 Dec. 2004	18	10 Jan. 2005	920	7600
E4971	F	855	5950	25 July 2003	13 July 2004	14 Dec. 2004	24	15 Aug. 2005	880	6850
E4970	F	865	5500	19 Dec. 2003	14 Dec. 2004		15	9 Aug. 2005	875	6500
E4973	F	795	5100	19 Dec. 2003	14 Dec. 2004		20	15 Aug. 2005	805	6800
C1998	F	960	8400	13 July 2004		14 Dec. 2004	14	7 Oct. 2005	970	8150
Wild sharks										
PJ622	F	393		11 Nov. 2004			5	9 Apr. 2005	377	
PJ45	F	394		9 Sept. 2004			11.1	9 Aug. 2005	445	
PJ788	F	771		13 Nov. 2004			6.8	4 June 2005	790	
PJ810	M	401		22 Jan. 2005			5.3	1 July 2005	430	
PJ826	M	445		21 Jan. 2005			5.4	3 July 2005	475	
PJ933	M	519		21 Jan. 2005			5.5	5 July 2005	539	
PJ597	M	557		13 Nov. 2004			6	13 May 2005	574	
PJ768	M	647		13 Nov. 2004			6.1	14 May 2005	660	

Note: OTC, oxytetracycline; ARS, Alizarin Red S.

width of the spine at its base, the pulp cavity is never completely filled by the inner TDL growth increments.

The fluorescent marks showed that the outer TDL grows only below the skin and mostly in the region close to the base of the spine where the odontoblasts are present (Maisey 1979). Consequently, cross sections at any level of the spine are unlikely to show all the outer TDL growth-increment bands. Sections close to the base of the spine may show the newest growth-increment bands in the outer TDL, whereas sections above the skin will show progressively earlier growth-increment bands farther up the spine trunk. This is consistent with the number of growth-increment bands in the outer TDL from any section along the spine being less than the number of bands in the inner TDL (Tovar-Ávila 2006). Clear sections at the very base of the spine were difficult to obtain because of the trunk in this region being thinner; it consists only of the new outer TDL growth-increment bands and it loses its form when cleaned and dried.

Our fluorescence results are consistent with the hypothesis that there are two TDLs in the spines of *H. portusjacksoni*, as proposed for some chondrichthyan species (Maisey 1979; Clarke et al. 2002*a*; Calis et al. 2005) rather than three TDLs as proposed for other chondrichthyans (Beamish and McFarlane 1985; Tanaka 1990; Irvine et al. 2006). The available evidence of growth regions based on injected specimens of *S. acanthias* (Beamish and McFarlane 1985) and *H. portusjacksoni* (present study) with OTC supports the interpretation that the appearance of a middle TDL is related to discontinuities in the inner TDL (Clarke et al. 2002*a*). The variable prominence of the discontinuity and its absence in some young specimens indicate that the discontinuity could be related to severe alterations in growth pattern through the life of the shark. Discontinuities in other calcified structures of fish, such as otoliths, are frequent and are attributed to alterations in growth pattern (e.g., adverse conditions or reproductive periods), and several types of discontinuities can be observed, from small gaps to major unconformities that can be traced

Fig. 2. Enamel band formation on the cap of the whole first dorsal-fin spine (female E4971, 855 mm total length, sacrificed August 2005) viewed under UV light with oxytetracycline (OTC) (*a*) and calcein filters (*b*). Scale bar = 0.5 mm.

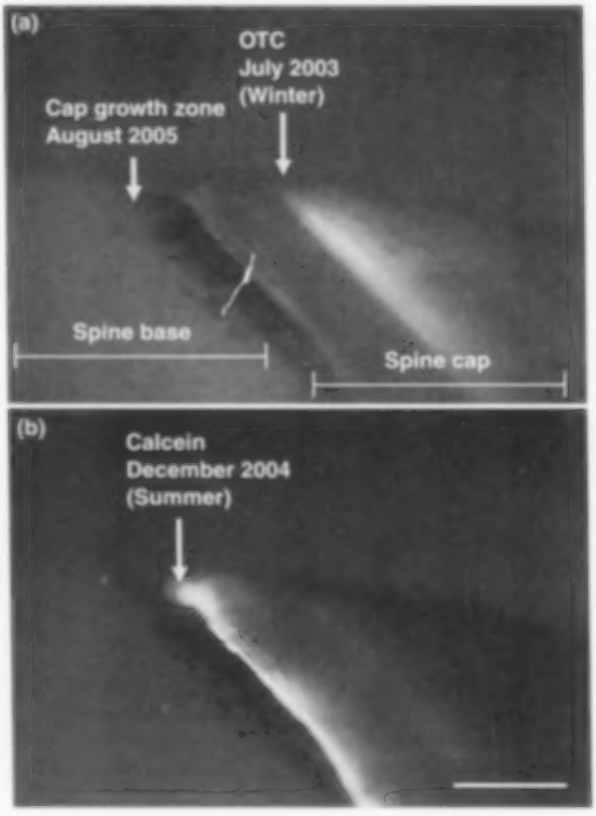

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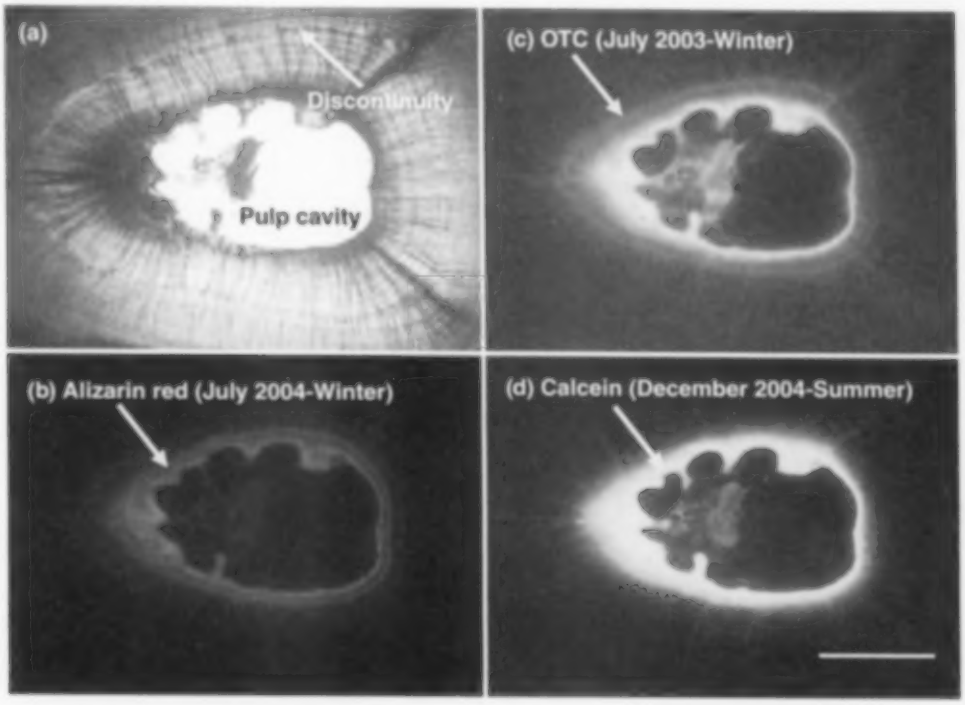
Fig. 3. Cross section of a dorsal-fin spine of a shark injected with oxytetracycline (OTC), Alizarin Red S, and calcein, viewed under white light (*a*) and UV light using different filters (*b*, *c*, and *d*), to show growth-increment band formation in the inner trunk dentine layer (female E4972, 906 mm total length, sacrificed January 2005). Remains of tissues in the pulp cavity show autofluorescence. Scale bar = 0.5 mm.



continuously along the entire calcified structure (Morales-Nin 1987).

If the separation between the inner and middle TDLs is only a major unconformity, studies considering the inner TDL as two separated layers for growth-increment band counts would underestimate shark age. Underestimation (rather than overestimation) of age inevitably produces demographic parameters that lead to overly optimistic prognoses in fishery stock assessment (Summerfelt and Hall 1987; Campana 2001).

Results from the present study are consistent with the concentric cones growth model of the spine proposed by Holden and Meadows (1962) for the growth of the inner TDL, but not for growth of the whole spine. Consistent with the results of Beamish and McFarlane (1985), our results do not support the Holden and Meadows conjecture that the inner TDL annuli (the cone bases) correspond to the annuli on the surface of the cap; however, nor do they correspond to the external bands as proposed by Beamish and McFarlane. Similar growth-increment band counts between the surface of trunk, the surface of the spine cap, and the inner TDL led Holden and Meadows to their interpretation, but Beamish and McFarlane (1985) provided evidence that the spine cap forms independently of the trunk. Beamish and McFarlane (1985) then assumed that the inner TDL annuli correspond to the external bands at the base of the spine as a result of discontinuous growth lengthening the spine. However, fluorescent marks in longitudinal sections and cross sections from our study show that the inner TDL grows along the entire length of the spine adjacent to the pulp cavity, which is consistent with the concentric cones growth model for the inner TDL, but never reaches the surface of the base of the spines to form the external bands because the outer TDL always surrounds the inner TDL.

The explanation of Beamish and McFarlane (1985) for the formation of growth-increment bands in the trunk appears to be correct only for the outer TDL, as they consist of layers deposited by the odontoblasts surrounding the trunk (Maisey 1979) at the base of the spine, growing in a differential way as the trunk moves away from the base. Therefore, each external band observed in the surface of the trunk corresponds to the upper limit of an outer TDL growth-increment band. These external bands become smaller and closer together as the shark growth diminishes in adults. In the present study, the external bands on the surface of the trunk were observed only on the part of the spine below the skin, because of difficulty in separating the cap from the trunk. A similar problem was found in *S. acanthias* (Beamish and McFarlane 1985).

The formation of enamel bands has been explained by an asynchronous growth of the cap and the spine trunk, where the cap downward growth is not reduced during periods of slow upward growth of the trunk (Beamish and McFarlane 1985), but this is inconsistent with both the cap and the spine trunk being subjected to the same mechanisms affect-

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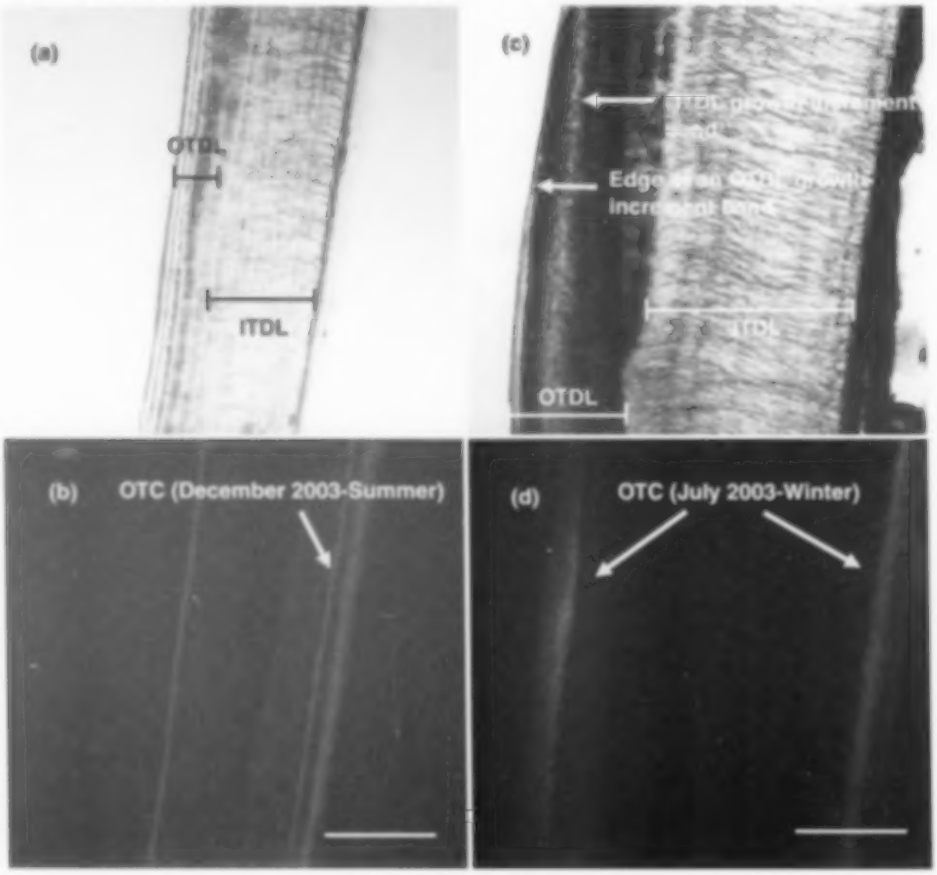
Fig. 4. Longitudinal sections showing the inner trunk dentine layer (ITDL) and outer trunk dentine layer (OTDL) at the middle level of the spine viewed under white light (*a*) and under UV light for the same section (*b*) to show the oxytetracycline (OTC) mark in the ITDL (female E4970, 865 mm total length, sacrificed August 2005). ITDL and OTDL at the base level of the spine viewed under white light (*c*) and under UV light for the same section (*d*) to show the OTC mark in both TDLs (female E4971, 855 mm total length, sacrificed August 2005). Autofluorescence can be seen in the edge of both TDLs in (*b*). Scale bars = 0.5 mm.



ing growth. Instead, enamel bands may well be related to a hypermineralization or accumulative process during periods of slow growth similar to that occurring in the growth-increment bands of vertebrae of teleosts (Morales-Nin 1987) and some chondrichthyans species such as *Mustelus antarcticus* (Officer et al. 1997). Beamish and McFarlane (1985) noted that the highest concentration of pigment and thickening of the enamel correspond to periods when the spine growth is reduced. Further studies on the hypermineralization of bands in chondrichthyan dorsal-fin spines are needed to clarify if the process is similar to other calcified structures.

The use of enamel bands of *S. acanthias* is suggested as the most convenient method to age this species, because the inner TDL annuli are less prominent (Beamish and McFarlane 1985). This is not the case for *H. portusjacksoni*, where growth increments in both spine growth zones are distinguishable. Furthermore, some deepwater dogfishes have a reduced spine cap with unclear annuli, which makes spine sectioning or the use of external bands the most suitable ageing methods (Clarke et al. 2002*a*, 2002*b*; Irvine et al. 2006). Large *S. acanthias* may also have a worn spine surface with no remaining pigment in distal portions of the spine cap (Holden and Meadows 1962; Ketchen 1975), so that the early enamel bands would be missed and alternative methods would be needed.

The positions of the fluorescent marks suggest that enamel bands form annually in the cap, whereas pairs of alternating opaque and translucent growth-increment bands formed annually in the TDLs of the spine. The spines of *H. portusjacksoni* appear to deposit a translucent growth-increment band in winter and an opaque band in summer, which is similar to the growth pattern observed in other chondrichthyan structures (Sullivan 1977; Cailliet and Goldman 2004). Full validation of ageing of *H. portusjacksoni* will require the analysis of growth-increment band formation in all age groups (Campana 2001).

In conclusion, dorsal-fin spines of *H. portusjacksoni* have three zones of simultaneous dentinogenesis causing its growth in different directions and only two dentine layers in

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Fig. 5. Cross section from a dorsal-fin spine viewed under white light (*a*) and the same section under UV light (*b*), showing the oxytetracycline (OTC) mark in the inner trunk dentine layer (ITDL), outer trunk dentine layer (OTDL), and mantle canals (MC), at the level of spine insertion in the skin (male PJ597, 574 mm total length, 181 days at liberty). Cross section viewed under UV light (*c* and *d*), showing the OTC mark in the ITDL and OTDL at the level of the base of the spine (*c*), and magnification of the inner rectangle (*d*) (male PJ810, 430 mm total length, 160 days at liberty). TP, trunk primordium; PC, pulp cavity; C, cap. Autofluorescence can be seen in the edge of both TDLs. Scale bars = 0.5 mm.

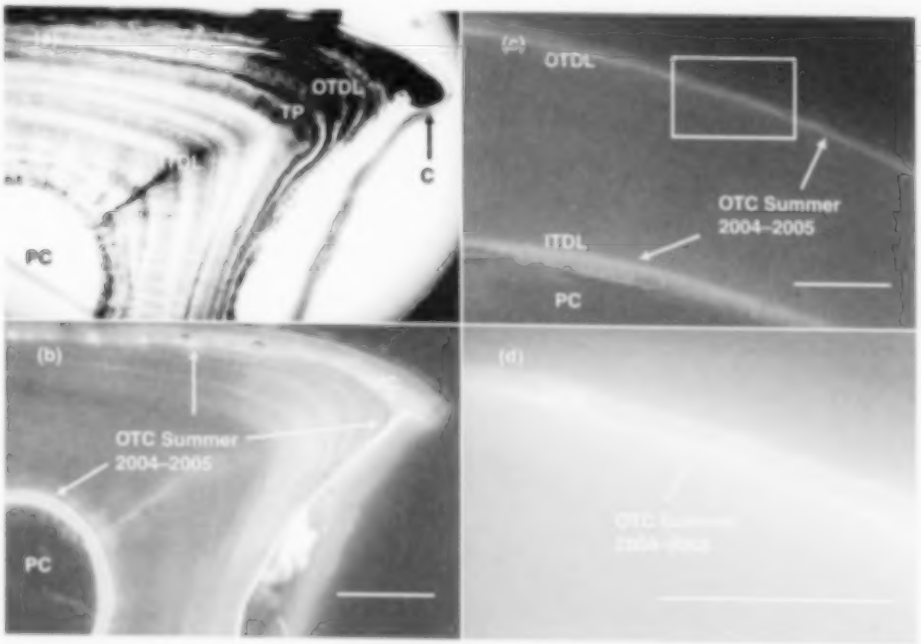
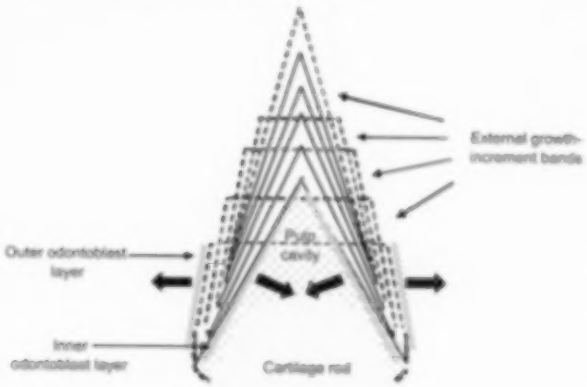


Fig. 6. Diagrammatic representation of the growth of a 5-year-old spine (considering the first growth increment or enamel band as the birth mark), based on Holden and Meadows (1962) concentric cones model for the inner trunk dentine layer. Thin solid lines represent growth-increment bands for the inner trunk dentine layer and dotted lines for the outer trunk dentine layer. Thick arrows show the regions and direction of growth of the trunk layers. Cap is not shown. Uncertain cartilage rod height is relative to the inner trunk dentine layer.



their trunk. Growth-increment bands from all the three growth zones: enamel bands, external bands resulting from the outer TDL growth-increment bands, and growth-increment bands in the inner TDL are potentially useful for age estimation because all of them are affected by the same endogenous and exogenous mechanisms involved in shark growth. Analogous morphology of dorsal-fin spines between heterodontid and squalid sharks (Maisey 1979), as well as some similarities with holocephalans (Calis et al. 2005), suggest that this model of growth devised for *H. portusjacksoni* could be applicable to all chondrichthyans possessing dorsal-fin spines. However, future research in other chondrichthyan groups is required to test the model.

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References

Beamish, R.J., and McFarlane, G.A. 1985. Annulus development on the second dorsal spine of the spiny dogfish (*Squalus acanthias*) and its validity for age determination. Can. J. Fish. Aquat. Sci. **42**: 1799–1805.

Braccini, J.M., Gillanders, B.M., Walker, T.I., and Tovar-Ávila, J. 2007. Comparison of deterministic growth models fitted to length-at-age data of the piked spurdog (*Squalus megalops*) in south-eastern Australia. Mar. Freshw. Res. **58**: 24–33.

Caillet, G., and Goldman, K.J. 2004. Age determination and validation in chondrichthyan fishes. *In* Biology of sharks and their relatives. *Edited by* J.C. Carrier, J.A. Musick, and M.R. Heithaus. CRC Press, Boca Raton, Fla., USA. pp. 399–447.

Calis, E., Jackson, E.H., Nolan, C.P., and Jeal, F. 2005. Preliminary age and growth estimates of the rabbitfish, *Chimaera monstrosa*, with implications for future resource management. J. Northwest Atl. Fish. Sci. **35**: 15–26.

Campana, S.E. 2001. Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. J. Fish Biol. **59**: 197–242.

Clarke, M.W., and Irvine, S.B. 2006. Terminology for the ageing of chondrichthyan fish using dorsal-fin spines. Environ. Biol. Fishes, **77**(3–4): 273–277.

Clarke, M.W., Connolly, P.L., and Bracken, J.J. 2002*a*. Age estimation of the exploited deepwater shark *Centrophorus squamosus* from the continental slopes of the Rockall Trough and Porcupine Bank. J. Fish. Biol. **60**: 501–514.

Clarke, M.W., Connolly, P.L., and Bracken, J.J. 2002*b*. Catch, discarding, age estimation, growth and maturity of the squalid shark *Deania calceus* in west and north Ireland. Fish. Res. **56**: 139–153.

Fielder, D.G. 2002. Methodology for immersion marking of walleye fry and fingerlings in oxytetracycline hydrochloride and its detection with fluorescence microscopy. Michigan Department of Natural Resources, Lansing, Mich., USA. Fish. Tech. Rep. 2002-1.

Holden, M.J., and Meadows, P.S. 1962. The structure of the spine of the spur dogfish (*Squalus acanthias* L.) and its use for age determination. J. Mar. Biol. Assoc. U.K. **42**: 179–197.

Irvine, S.B., Stevens, J.D., and Laurenson, L.J.B. 2006. Surface bands on deepwater squalid dorsal-fin spines: an alternative method for ageing *Centroselachus crepidater*. Can. J. Fish. Aquat. Sci. **63**: 617–627.

Izzo, C., Rodda, K., and Bolton, T. 2007. Incorporation time of oxytetracycline into calcified structures of the elasmobranch *Heterodontus portusjacksoni*. J. Fish Biol. **71**: 1208–1214.

Ketchen, K.S. 1975. Age and growth of dogfish *Squalus acanthias*, in British Columbia waters. J. Fish. Res. Board Can. **32**: 43–59.

Last, P., and Stevens, J. 1994. Sharks and rays of Australia. CSIRO Publishing, Melbourne, Australia.

Logsdon, D.E., Pittman, B.J., and Barnard, G.C. 2004. Oxytetracycline marking of newly hatched walleye fry. N. Am. J. Fish. Manag. **24**: 1071–1077.

Maisey, J.G. 1979. Finspine morphogenesis in squalid and heterodontid sharks. Zool. J. Linn. Soc. Lond. **66**: 161–183.

Morales-Nin, B. 1987. Ultrastructure of the organic and inorganic constituents of the otoliths of the sea bass. *In* Age and growth of fish. *Edited by* R.C. Summerfelt and G.E. Hall. Iowa State University Press, Ames, Iowa. pp. 331–343.

Officer, R.A. 1995. Vertebral mineralization patterns in gummy and school sharks and their utility for age determination. Ph.D. thesis, Department of Zoology and School of Dental Science, University of Melbourne, Australia.

Officer, R.A., Day, R.W., Clement, J.G., and Brown, L.P. 1997. Captive gummy sharks, *Mustelus antarcticus*, form hypermineralised bands in their vertebrae during winter. Can. J. Fish. Aquat. Sci. **54**: 2677–2683.

Smith, S.E., Mitchell, R.A., and Fuller, D. 2003. Age-validation of a leopard shark (*Triakis semifasciata*) recaptured after 20 years. Fish. Bull. **101**: 194–198.

Sullivan, K.J. 1977. Age and growth of the elephant fish *Callorhinchus milii* (Elasmobranchii: Callorhynchidae). N.Z. J. Mar. Freshw. Res. **11**(4): 745–753.

Summerfelt, R.C., and Hall, G.E. (*Editors*). 1987. Age and growth of fish. Iowa State University Press, Ames, Iowa.

Tanaka, S. 1990. The structure of the dorsal spine of the deep sea squaloid shark *Centrophorus acus* and its utility for age determination. Nippon Suisan Gakkaishi, **56**(6): 903–909.

Tovar-Ávila, J. 2006. Reproduction, age validation, growth determination and effects of fishing on the Port Jackson shark (*Heterodontus portusjacksoni*) in South-eastern Australia. Ph.D. thesis, Department of Zoology, University of Melbourne, Australia.

Walker, T.I., Officer, R.A., Clement, J.G., and Brown, L.P. 1995. Southern shark age validation. Part 1. Project overview, vertebral structure and formation of growth-increment bands used for age determination. Final report to Fisheries Research and Development Corporation (FRDC Project 91/037). Department of Conservation and Natural Resources, East Melbourne, Victoria, Australia.

Walker, T.I., Hudson, R.J., and Gason, A.S. 2005. Catch evaluation of target, by-product and bycatch species taken by gillnets and longlines in the shark fishery of south-eastern Australia. J. Northwest Atl. Fish. Sci. **35**: 505–530.

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Water-yield estimates for critical loadings assessment: comparisons of gauging methods versus an isotopic approach

K.E. Bennett, J.J. Gibson, and P.M. McEachern

Abstract: An isotope mass balance technique is applied to quantify water yield and refine a steady-state critical acid loadings assessment for 49 lakes in hydrologically complex, wetland-rich terrain of northeastern Alberta. The approach uses physical and climatological data combined with site-specific measurements of evaporative isotopic enrichment of ^{2}H and ^{18}O in lake water to measure lake residency and ungauged runoff to lakes. Mean water yields to individual lakes across the region over a 3-year period are estimated to range from 5 to 395 mm·year^{-1}, with a standard deviation of two times the predicted estimates based on interpolation of gauged stream flow from broad-scale watersheds in the area. Comparison of the method with longer-term Water Survey of Canada hydrometric data suggests very similar average water yields for moderate- to large-sized watersheds. However, the isotope-based estimates appear to capture extreme low water yields in flat, disconnected areas and extreme high water yields in other areas thought to be related to stronger connections to regional groundwater flow systems. For aquatic ecosystems of northeastern Alberta, an area expected to be affected by acid deposition from regional oil sands development, continued refinement of the technique is important to accurately assess critical loads for ungauged systems, particularly those in low-yield settings.

Résumé : Une technique de bilan massique isotopique nous permet de quantifier le rendement en eau et de raffiner une évaluation à l'état d'équilibre des charges acides critiques de 49 lacs sur un terrain riche en terres humides et à hydrologie complexe dans le nord-est de l'Alberta. Notre méthodologie utilise des données physiques et climatologiques, de même que des mesures spécifiques au site de l'enrichissement isotopique en ^{2}H et en ^{18}O dans l'eau de lac dû à l'évaporation, afin de mesurer la durée de résidence dans les lacs et le ruissellement non jaugé vers les lacs. Nous estimons que l'apport moyen d'eau aux lacs individuels dans toute la région sur une période de trois ans varie de 5 à 395 mm·an^{-1}, avec un écart type de deux fois les estimations prédites d'après des interpolations des débits jaugés de ruisseaux faites dans des bassins versants à grande échelle de la région. Une comparaison de notre méthode avec les données hydrométriques à plus long terme des Relevés hydrologiques du Canada montre des rendements moyens en eau très semblables pour les bassins versants de taille moyenne à supérieure. Les estimations basées sur les isotopes semblent indiquer des apports d'eau extrêmement faibles pour les régions plates et isolées et des apports extrêmement élevés pour d'autres régions qu'on croit posséder des connections plus importantes avec les systèmes régionaux d'eaux souterraines. Dans le cas des écosystèmes aquatiques du nord-est de l'Alberta, qu'on croit devoir être affectés par les précipitations acides produites par le développement des sables bitumineux de la région, il est important de raffiner la méthodologie afin d'évaluer les charges critiques dans les systèmes non jaugés, particulièrement ceux qui se situent dans des conditions d'apports d'eau faibles.

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Introduction

Previous studies have indicated that lakes and ponds in northeastern Alberta, the hub of oil sands mining and refinery operations in Canada, may be sensitive to acidifying emissions due to the prevalence of acid-sensitive soils and aquatic features common to the region (e.g., Erickson 1987; Schindler 1996). Recent growth in the rate and extent of oil sands development, and commensurate increases in NO_x and SO_x emissions from refinery operations centred near the town of Fort McMurray, are intensifying this concern. Although impacts to aquatic ecosystems are not widely reported at present, there remains a lack of scientific information to evaluate suitable environmental thresholds and ensure that emissions targets are adequately protecting aquatic and terrestrial ecosystems in the long term. Through its NOx SOx Working Group, the Cumulative Environmental Management Association (CEMA), a multi-stakeholder NGO, is currently sponsoring research into the potential sensitivity of the local environment, including assessment of critical loads of acidifying emissions to aquatic ecosystems. Critical loads represent a limit or threshold for atmospherically deposited sulphur and nitrogen that ensure long-term sustainability of the targeted ecosystem. A first approximation of critical acid loads (CL_A) to lakes in the area was undertaken for 449 lakes and ponds in the region using the steady-state water chemistry model (SSWC; Henriksen et al. 1992; Western Resource Solutions (WRS) 2004). The calculated critical loads were exceeded by predicted potential acid input for 17 of the 449 lakes, but with considerable uncertainty due to a number of poorly known factors, primary among them being actual acid deposition and, on the receptor side, water yield. This paper focuses on investigating the hydrological controls at 50 select lake sites, i.e., water-yield factors and how they affect such critical loadings assessments.

Water yield is a difficult parameter to estimate because of the sparsity of the hydrometric network in northern Alberta and, as shown in this paper, the high lake-to-lake variability in runoff, which may reduce the robustness of interpolating between gauging stations. As long-term hydrometric networks were also designed to gauge large-scale runoff in rivers rather than discharge from individual lakes, direct application of discharge data to lakes must be scrutinized cautiously.

Accuracy of the critical acid load estimate by the SSWC model is directly proportional to accurate estimates of water yield (W_Y). Use of in situ isotope measurements provides a sharper focus on water yield than extrapolation from conventional hydrometric monitoring in the area, which can be useful for assessing sensitivity of individual lakes to acid deposition. For a regional subset of the 449 previously studied systems (WRS 2004), an isotope mass balance technique was applied using $\delta^{18}O$ and $\delta^{2}H$ of Gibson et al. (2002), which utilizes the systematic isotopic fractionation that occurs during evaporation to estimate the lake residence time, and the required water yield from the catchment to sustain the observed isotopic balance. Results of the isotopic approach are compared with those from conventional hydrometric techniques to test the implications for critical acid loadings models to illustrate potential errors and limitations in the approaches. This examination also lends insight into scale-dependent landscape features that affect the way in which water is processed and removed from the landscape in boreal forest terrain.

The objectives of this paper are to compare water-yield results obtained from conventional and isotopic methods, to demonstrate their incorporation into a preliminary critical acid loadings assessment, and to highlight the sensitivity of the critical acid loadings model to hydrological controls across a regional domain. This phase of the research does not attempt to use dynamic models to address rapidly fluctuating water balance parameters (for a recent example south of this region, see Smerdon et al. 2007). The results from this preliminary analysis are anticipated to be useful for improving regional perspectives of lake acidification potential, particularly in complex, wetland-rich terrain, and establishing potential for broader incorporation into aquatic ecosystem assessments.

Materials and methods

Site description

The lakes under study are located in northeastern Alberta, Canada (55°30′N to 60°N, 30′W; Fig. 1; Table 1). Thirty lakes are situated within 200 km of Fort McMurray and its nearby oil sands developments. Five lakes are found in the Caribou Mountains and four lakes are situated above Lake Athabasca. All are primarily located in headwater catchments and range in size from shallow, small ponds (1 m depth, <0.5 km^2) to large lakes (30 m depth, 43 km^2), with average lake depth and size equal to 4.3 m and 3 km^2, respectively. The lakes were part of an on-going monitoring program of acid-sensitive lakes in Alberta carried out by Alberta Environment and the Regional Aquatics Monitoring Program (RAMP 2004). All lake chemistry data derive from RAMP and a discussion of collection and analysis of water samples for chemistry is reported elsewhere (RAMP 2006). These chemistry data are publicly available from Alberta Environment.

Air temperature normal (1971–2000) at Fort McMurray is 0.7 °C, whereas the average open-water season (May to October) temperature is 11.6 °C. Mean annual precipitation is 456 mm, 69% of which falls as rain during the May to October period (Meteorological Service of Canada 2004). Average annual evaporation is 480 mm (Hamon 1961; New et al. 1999), and evaporation from lakes has been estimated at 578 mm (Bothe and Abraham 1987, 1993). Relative humidity during the open-water period is close to 68%.

Temperature, precipitation, and snowfall for the study years (2001–2004) were calculated based on the October to September water year and compared with the long-term mean values at the Fort McMurray climate station using the R package "seas" (Toews et al. 2007). Study season November through January and midsummer (June and July) daily mean temperatures are, on average, 0.2–3.6 °C warmer, whereas spring and late summer – early fall months (August to October) are generally cooler on average (–2.6 to –0.4 °C) compared with the long-term average (1944–2004) conditions, with the greatest differences observed during the winter (+3.6 °C) and spring (–2.6 °C) seasons (Table 2). Daily total precipitation is less variable than temperature between

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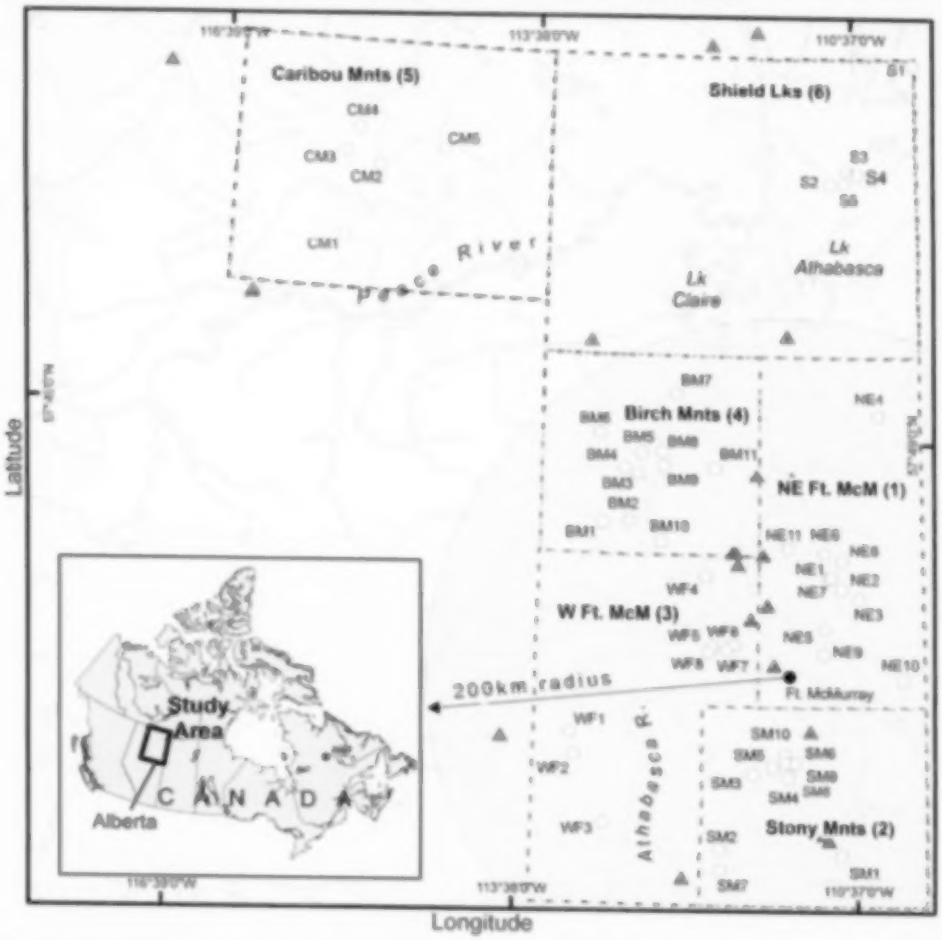
Fig. 1. Map of study regions, lakes, Water Survey of Canada gauges, and major rivers. Lake sites are shown as open circles, and WSC gauges are indicated by shaded triangles. The shaded area indicates the 200 km radius, which includes Fort McMurray's (Ft. McM) associated oil sands developments and all lakes that are considered to fall within the area most likely to be impacted by oil sands development. Inset illustrates location of site in Alberta and Canada. Mnts, Mountains; Lks, Lakes.



study years and the long term; the greatest difference in precipitation occurs in the summer season (–25.5 mm; Table 2). Differences in total snowfall are reflective of temperature variations during the study season versus the long-term average, higher mean temperatures in November and December lead to less snow (–10.8 cm).

Long-term (1962–2004) average monthly flow (March to October open-water season) was compared with the study season (2002–2004) average monthly flow at active WSC gauges (13) used in this study. Annual total hydrologic flow is lower on average (10.6 $m^3 \cdot s^{-1}$ vs. 11.6 $m^3 \cdot s^{-1}$) by 1 $m^3 \cdot s^{-1}$, with the exception of the month of October when flows are slightly higher (Fig. 2).

The lakes are grouped within six regional study areas: (1) northeast (NE) Fort McMurray; (2) Stony Mountains; (3) west Fort McMurray; (4) Birch Mountains; (5) Caribou Mountains; and (6) Shield Lakes. Study areas range in elevations from 200 m (region 6) to 1000 m (region 5), with similar average elevations occurring within regions 1 and 3 and regions 2 and 4. Average slopes (based on DEM analysis in a geographic information system) within study catchments are low, ranging from 0.5% in region 3 to 5.4% in region 5, with higher average slopes occurring in the watersheds of regions 5 and 6 and regions 2 and 1. There is a wide range of variation present within the lake sites, including their latitudinal position, morphometry, and the landscapes within which they are situated (Table 1).

Regional surficial materials consist primarily of thick tills (65%), till veneers (21%), with some coarse sands and silts (3%), and minor amounts of sands and gravel, as well as fine silts and clay (Fulton 1996). Soils in regions 1, 2, 3, and 4 are comprised of organics, luvisols, brunisols, and cryosols (region 4), whereas cryosols and regosols are dominant soil types in regions 5 and 6, respectively (Shields et al. 1991; Soil Landscapes of Canada Working Group 2005). Permafrost is sporadic discontinuous (10%–50%), with low ground ice content (<10%) at the Shield and Taiga Plain sites, and in the remainder of the sites, permafrost is either absent or

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Table 1. Location, position, and areal extent of study lakes and catchment areas.

Lake no.	Latitude (N)[a]	Longitude (W)[a]	Lake surface area (m^2)	Catchment area (m^2)	Maximum lake depth (m)	Lake volume (m^3)
Region 1: NE Fort McMurray						
NE1	57.15	110.85	652 300	13 111 800	1.83	783 100
NE2	57.09	110.75	336 700	16 987 500	1.83	427 900
NE3	57.96	110.40	1 162 400	15 978 100	1.22	713 500
NE4	57.05	110.59	581 800	6 635 400	2.13	842 500
NE5	56.89	110.90	1 894 900	19 573 200	1.83	1 731 200
NE6	57.27	110.90	372 900	10 682 600	1.39	327 800
NE7	57.15	110.86	111 900	4 073 300	2.00	112 300
NE8	57.23	110.75	114 600	6 470 400	1.22	92 100
NE9	56.77	110.91	3 154 800	20 090 300	1.83	3 517 800
NE10	56.64	110.20	4 188 000	27 669 900	1.50	3 227 700
NE11	57.29	111.24	5 753 200	68 918 300	3.50	7 614 500
Region 2: Stony Mountains						
SM1	55.76	110.76	2 369 500	7 085 700	1.83	1 594 200
SM2	55.79	111.83	1 973 800	24 292 300	1.22	1 126 100
SM3	56.20	111.37	1 861 300	7 677 300	3.05	2 691 700
SM4	56.15	111.23	525 600	11 998 500	1.22	371 100
SM5	56.17	111.55	1 061 000	6 291 900	1.83	1 219 500
SM6	56.22	111.17	699 200	3 393 600	1.52	617 900
SM7	55.68	111.83	1 476 100	5 782 400	3.00	1 885 700
SM8	56.21	111.20	1 912 500	9 719 800	2.50	1 694 600
SM9	56.22	111.25	1 071 400	9 470 800	1.20	608 000
SM10	56.26	111.26	1 352 100	17 390 500	1.22	933 700
Region 3: West Fort McMurray						
WF1	56.35	113.18	3 203 400	24 212 800	1.22	1 874 800
WF2	56.24	113.14	755 100	23 370 200	1.80	707 900
WF3	55.91	112.86	2 163 500	38 142 700	2.00	2 090 700
WF4	57.15	111.98	34 200	1 790 600	1.50	28 600
WF5	56.80	111.92	234 500	6 887 800	1.22	176 700
WF6	56.81	111.72	182 300	5 121 700	1.52	177 500
WF7	56.78	111.79	85 000	1 711 700	1.22	67 500
WF8	56.77	111.95	2 025 000	27 074 100	1.52	1 457 700
Region 4: Birch Mountains						
BM1	57.41	112.93	17 029 700	51 318 200	9.14	98 076 200
BM2	57.42	112.69	43 974 800	119 642 300	27.43	454 190 300
BM3	57.65	112.62	965 600	28 621 000	4.57	1 333 700
BM4	57.69	112.74	4 264 100	34 097 900	1.22	1 828 200
BM5	57.76	112.58	2 636 900	27 892 300	1.22	1 204 300
BM6	57.85	112.97	1 290 200	18 397 900	0.91	639 900
BM7	58.06	112.27	676 900	7 812 200	1.50	446 000
BM8	57.77	112.40	1 215 100	32 684 100	1.83	1 358 900
BM9	57.70	112.38	3 484 800	30 261 500	10.67	11 147 600
BM10	57.31	112.40	393 700	5 094 600	1.50	145 600
BM11	57.69	111.91	55 000	1 478 900	5.00	13 100
Region 5: Caribou Mountains						
CM1	58.77	115.44	1 600 400	23 934 700	8.50	10 332 000
CM2	59.13	115.13	9 550 300	37 926 800	6.00	27 318 000
CM3	59.19	115.46	2 300 100	25 257 900	1.50	4 030 800
CM4	59.31	115.35	2 627 800	35 818 200	16.00	21 733 200
CM5	59.24	114.53	552 300	2 575 500	1.50	865 200
Region 6: Shield Lakes						
S1	59.72	110.02	3 404 900	13 398 600	27.43	22 492 400
S2	59.12	110.83	1 025 200	110 260 700	12.19	3 607 000
S3	59.19	110.68	1 447 900	29 694 400	10.67	4 842 000
S4	59.17	110.57	1 416 300	123 079 400	9.14	5 644 000
S5	59.13	110.69	316 700	4 477 400	8.53	312 800

[a]Latitude and longitude are given in decimal degrees.

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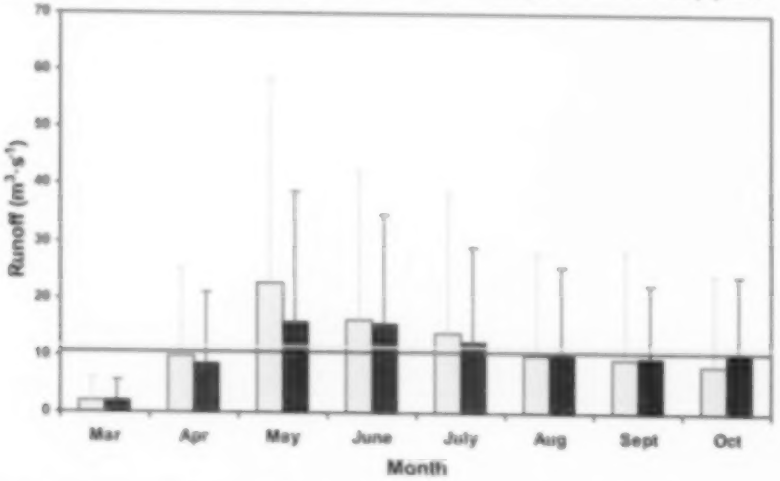
Table 2. Differences in daily long-term climate (1944–2004) and the study years (2002–2004) at the Fort McMurray climate station.

Month	Season	Minimum temperature (°C)	Mean temperature (°C)	Maximum temperature (°C)	Total precipitation (mm)	Total snow (cm)
December	Winter	3.4	3.6	3.8	–10.3	–10.1
January		2.0	1.4	0.9	0.1	–1.3
February		1.5	1.7	2.0	0.1	1.4
March	Spring	–3.1	–2.6	–2.0	–0.7	–0.6
April		–1.2	–0.9	–0.7	–7.1	–5.1
May		–2.6	–2.4	–2.2	6.7	5.5
June	Summer	–0.9	0.2	1.2	–14.4	0.0
July		0.6	0.8	1.1	6.9	0.0
August		–1.0	–0.7	–0.3	–25.5	0.0
September	Fall	–0.1	–0.4	–0.7	10.4	–1.0
October		–2.0	–1.8	–1.6	7.9	3.0
November		2.7	2.7	2.7	–3.9	–11.5

Note: Snow is the difference between the study years (2001–2004) to account for preseason snowfall.

Fig. 2. Hydrologic range of runoff measured over the long term (1962–2004, light gray bars) and for the three years of study (2002–2004, dark gray bars). Error bars indicate runoff variability +1 SD for both the long term and the study years.



only in isolated patches (0%–10%), with low or low-to-nil ground ice (Brown et al. 1998). The overall study area comprises 13% bogs, 22% fens, and 65% mineral upland. Peatland coverage in specific watersheds varies considerably, but the regional averages are fairly representative of the broader terrain under investigation (see Vitt et al. 1996).

Physical data collection

Water samples were collected in the late summer – early fall during 2002, 2003, and 2004. The 2004 seasonal program (Alberta Environment public water data archives) sampled a subset of 10 lakes and ponds from the 50-lake population and provided support for the hypothesis that lakes in the Wood Buffalo region exhibit annual isotopic highs (peak enrichment) during this time period (see discussion of this issue in Gibson et al. 2002). However, more detailed study of the study lakes in terms of seasonal flux is required. Lake samples were collected from the pontoon of a fixed-wing aircraft, and helicopters were used to access ponds and terrestrial monitoring sites. For lakes greater than 2 m in depth, a composite water sample was collected at the deepest part of the lake by multiple hauls of a polyvinyl chloride tube to the euphotic depth (two times the secchi disk depth) or 1 m above the lake bottom. For lakes less than 2 m deep, a composite sample was created from five 1 L collections at 0.5 m depths from different locations around the lake. Water was transferred from the composite sample to a 30 mL high-density polyethylene bottle, which was tightly sealed and sent to the University of Waterloo (Waterloo, Ontario) for analysis of $\delta^{18}O$ and $\delta^{2}H$ by standard isotope ratio mass spectrometry methods. All δ isotope results are given in per mil (‰) vs. VSMOW (Vienna Standard Mean Ocean Water; see Coplen 1996).

Watershed and lake physical parameters were estimated within a geographic information system (GIS) using 1:10 000 orthophotography and digital elevation models (DEMs) (1:20 000) to digitize lake surface area, drainage basin morphometry, and lake surface elevation. Lake bathymetry was characterized from three to five multiple transects across lake sites

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Table 3. Summary of input values for ^{18}O mass balance (IMB).

	Interpolated					Calculated				Measured		Modelled	
Lake no.	P (mm)	E (mm)	T (°C)	h	δ_p (‰)	ε^* (‰)	ε_k (‰)	ε (‰)	m	$\bar{\delta}_L$ (‰)	±1 SD (‰)	δ_s (‰)	δ^* (‰)
Region 1: NE Fort McMurray													
NE01	417	434	12.25	0.67	−18.54	10.45	4.66	15.11	1.97	−15.05	0.78	−23.59	−1.11
NE02	419	434	12.08	0.67	−18.61	10.47	4.66	15.13	1.97	−15.40	0.86	−23.57	−1.07
NE03	379	430	12.61	0.67	−18.51	10.41	4.64	15.06	1.98	−14.44	0.47	−23.89	−1.56
NE04	429	432	12.10	0.67	−18.58	10.46	4.67	15.13	1.97	−13.00	0.11	−23.55	−1.04
NE05	424	436	12.37	0.67	−18.25	10.44	4.68	15.12	1.96	−11.09	0.37	−23.47	−0.93
NE06	409	435	12.24	0.67	−18.54	10.45	4.66	15.11	1.97	−13.94	0.96	−23.64	−1.17
NE07	417	434	12.25	0.67	−18.53	10.45	4.67	15.12	1.97	−16.12	0.74	−23.58	−1.09
NE08	414	434	12.24	0.67	−18.50	10.45	4.66	15.11	1.97	−14.66	0.94	−23.62	−1.16
NE09	436	440	12.47	0.67	−18.17	10.43	4.70	15.12	1.95	−9.24	0.27	−23.41	−0.83
NE10	444	432	12.46	0.67	−18.09	10.43	4.69	15.11	1.96	−9.13	0.86	−23.36	−0.82
NE11	404	437	12.81	0.67	−18.18	10.39	4.67	15.06	1.97	−12.44	0.18	−23.60	−1.19
Region 2: Stony Mountains													
SM01	458	448	12.17	0.67	−17.87	10.46	4.65	15.10	1.98	−8.66	0.54	−23.02	−0.58
SM02	472	457	11.69	0.68	−18.11	10.50	4.58	15.08	2.03	−7.68	1.04	−23.06	−0.82
SM03	458	447	11.78	0.67	−18.36	10.49	4.63	15.13	1.99	−9.79	0.15	−23.23	−0.80
SM04	458	447	11.76	0.67	−18.34	10.50	4.64	15.13	1.99	−11.00	0.89	−23.21	−0.75
SM05	462	449	11.79	0.67	−18.34	10.49	4.62	15.11	2.00	−9.63	0.30	−23.21	−0.83
SM06	457	446	11.85	0.67	−18.36	10.49	4.64	15.13	1.98	−10.47	0.39	−23.23	−0.77
SM07	478	459	11.67	0.68	−18.02	10.51	4.57	15.08	2.03	−8.01	0.74	−23.02	−0.79
SM08	457	447	11.79	0.67	−18.36	10.49	4.64	15.13	1.99	−10.26	0.40	−23.23	−0.78
SM09	457	447	11.74	0.67	−18.37	10.50	4.64	15.14	1.99	−11.51	0.17	−23.24	−0.78
SM10	455	446	11.69	0.67	−18.40	10.50	4.64	15.14	1.99	−12.07	0.24	−23.26	−0.78
Region 3: West Fort McMurray													
WF01	448	457	12.00	0.68	−18.25	10.47	4.48	14.96	2.09	−8.69	0.89	−23.27	−1.45
WF02	448	458	11.94	0.68	−18.23	10.48	4.48	14.96	2.09	−8.19	0.56	−23.23	−1.42
WF03	454	462	12.00	0.68	−17.94	10.47	4.51	14.99	2.07	−9.51	1.20	−23.09	−1.15
WF04	416	447	12.61	0.68	−18.16	10.41	4.61	15.02	2.01	−8.71	0.47	−23.56	−1.36
WF05	427	447	12.45	0.67	−18.29	10.43	4.62	15.05	2.00	−9.37	0.64	−23.43	−1.15
WF06	430	444	12.65	0.67	−18.20	10.41	4.64	15.05	1.98	−11.59	1.37	−23.42	−1.07
WF07	431	447	12.51	0.67	−18.26	10.42	4.63	15.05	1.99	−11.52	1.41	−23.41	−1.10
WF08	430	447	12.39	0.68	−18.26	10.44	4.61	15.05	2.00	−8.32	0.42	−23.42	−1.15
Region 4: Birch Mountains													
BM01	407	451	11.24	0.68	−19.13	10.55	4.48	15.03	2.09	−12.71	0.17	−23.76	−1.86
BM02	408	452	11.47	0.68	−19.00	10.53	4.49	15.02	2.08	−12.31	0.13	−23.75	−1.82
BM03	398	454	11.41	0.68	−19.06	10.53	4.50	15.03	2.08	−14.93	0.68	−23.85	−1.89
BM04	396	453	11.41	0.68	−19.03	10.53	4.49	15.03	2.08	−12.29	0.90	−23.87	−1.93
BM05	393	454	11.36	0.68	−19.10	10.54	4.50	15.04	2.08	−13.19	1.00	−23.90	−1.93
BM06	389	451	11.34	0.68	−19.24	10.54	4.48	15.02	2.09	−15.28	0.64	−23.94	−2.05
BM07	382	447	11.47	0.68	−19.42	10.53	4.52	15.04	2.07	−14.86	0.35	−24.02	−2.01
BM08	392	454	11.35	0.68	−19.07	10.54	4.51	15.05	2.07	−15.03	0.57	−23.91	−1.90
BM09	395	453	11.37	0.68	−19.20	10.54	4.51	15.05	2.07	−13.79	0.49	−23.88	−1.86

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Table 3 (*concluded*).

	Interpolated				Calculated				Measured		Modelled	
Lake no.	P (mm)	E (mm)	T (°C)	h	δ_P (‰)	ε^* (‰)	ε_k (‰)	ε (‰)	m	δ_L (‰)	±1 SD (‰)	δ_A (‰)	δ^* (‰)
BM10	413	451	11.97	0.68	−18.69	10.48	4.54	15.01	2.05	−8.59	0.45	−23.67	−1.64
BM11	390	445	11.58	0.68	−19.28	10.51	4.55	15.07	2.04	−11.54	0.61	−23.86	−1.71
Region 5: Caribou Mountains													
CM01	383	449	10.96	0.68	−19.99	10.58	4.50	15.07	2.08	−16.11	0.19	−24.35	−2.35
CM02	368	437	10.38	0.69	−20.26	10.63	4.42	15.06	2.13	−13.21	0.32	−24.54	−2.73
CM03	364	436	10.41	0.69	−20.28	10.63	4.45	15.08	2.11	−14.39	0.73	−24.56	−2.66
CM04	356	434	10.44	0.69	−20.33	10.63	4.43	15.06	2.13	−16.21	0.26	−24.61	−2.78
CM05	354	433	10.80	0.69	−20.04	10.59	4.40	14.99	2.15	−12.00	0.68	−24.55	−2.89
Region 6: Shield Lakes													
S01	345	391	11.93	0.68	−19.38	10.48	4.53	15.01	2.06	−12.30	0.20	−24.67	−2.68
S02	356	409	12.16	0.68	−19.06	10.46	4.55	15.01	2.04	−15.73	0.14	−24.41	−2.37
S03	356	401	12.12	0.68	−19.11	10.46	4.55	15.01	2.05	−15.04	0.30	−24.44	−2.41
S04	360	401	12.30	0.68	−18.99	10.44	4.56	15.00	2.04	−13.50	0.34	−24.42	−2.38
S05	359	407	12.18	0.68	−19.08	10.46	4.56	15.01	2.04	−12.53	0.12	−24.41	−2.35

Note: P, precipitation on the lake; E, lake evaporation; T, temperature; h, relative humidity; δ_P, δ_L, and δ_A, isotopic composition of precipitation, lake water, and the atmosphere, respectively; δ^*, limiting isotopic enrichment; ε, liquid–vapour isotopic separation factor; ε^* and ε_k, the temperature-dependent equilibrium and transfer-mechanism dependent kinetic separations, respectively; m, enrichment slope; SD, standard deviation.

using a sounder to record depth at 15-s time intervals and a Garmin handheld global positioning system (GPS) to record position for each transect. Raw data was contoured and converted to lake volume based on the surface area of slices at discrete depth intervals and geometric assumptions for frustral volumes. Lake centroids were used to generate specific latitude and longitude positions for interpolation of variables such as temperature from gridded climate data sets.

Methodology for model parameterization

Runoff and water-yield estimates were generated using an isotope mass balance model (IMB), developed under the assumptions of complete vertical mixing, constant density of water, and steady-state conditions, shown to be a reasonable approximation for typical lakes in the area (Gibson et al. 2002). In hydrologic and isotopic steady state, water and isotope balances are expressed, respectively, as

$$(1) \qquad P + W_Y - Q - E = 0$$

$$(2) \qquad P\delta_P + W_Y\delta_{WY} - Q\delta_Q - E\delta_E = 0$$

where P is precipitation on the lake (m^3), W_Y is catchment water yield, including both surface and groundwater fluxes to the lake (m^3), Q is the lake discharge, including surface and groundwater fluxes from the lake, and E is lake evaporation (m^3). Isotopic variables include δ_P, δ_{WY}, δ_Q, δ_E, the isotopic composition of precipitation, catchment water yield, discharge, and evaporation flux, respectively. The latter is observed to be substantially depleted in heavy isotopes under natural evaporation conditions because of kinetic isotopic fractionation that arises during diffusion of water vapour in air. δ_E was estimated using a simplified version of the one-dimensional Craig–Gordon diffusion model (see Gat 1996), which requires estimates of air temperature, humidity, the isotopic composition of atmospheric moisture δ_A, and the liquid–vapour isotopic separation factors $\varepsilon = \varepsilon^* + \varepsilon_k$, where ε^* and ε_k are the temperature-dependent equilibrium and transfer-mechanism-dependent kinetic separations, respectively, established and widely used from laboratory and wind tunnel experiments (Merlivat and Coantic 1975; Horita and Wesolowski 1994), the latter being representative of boundary-layer conditions for lakes on water budget time scales (Gonfiantini 1986). Several additional simplifications are made to compute the IMB: (*i*) the isotopic composition of catchment water yield is equal to that of precipitation, i.e., $\delta_{WY} = \delta_P$ as would be valid where runoff is locally derived from recent meteoric water that has not undergone substantial isotopic enrichment; (*ii*) the isotopic composition of discharge is adequately characterized by the isotopic signature of lake water δ_L, expected for well-mixed lakes; and (*iii*) lake water is adequately described by the mean isotopic composition of 3 years of late-summer sampling, which has been discussed previously (Gibson et al. 2002).

Rearranging and simplifying eq. 2, substituting $Q = P + W_Y - E$ from eq. 1, $\delta_E = (\delta_L - h\delta_A - \varepsilon)/(h - \varepsilon)$ from Gat (1995), and $\delta_{WY} = \delta_P$, $\delta_Q = \delta_L$ yields an estimate of the fraction of water loss by evaporation ($x = E/(P + W_Y)$) expressed as

$$(3) \qquad x = \frac{(\delta_L - \delta_P)}{m(\delta^* - \delta_L)}$$

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where $m = (h - \varepsilon)/(1 - h + \varepsilon_K)$ is the enrichment slope, h is the humidity (relative humidity × 100), and $\delta^* = (h\delta_A + \varepsilon)/(h - \varepsilon)$ is the limiting isotopic enrichment.

Data used in the IMB are provided in Table 3. For computing x using eq. 3, atmospheric variables such as temperature, used to calculate the equilibrium separation ε^*, humidity h, the kinetic fractionation ε_K, and hence, m, δ^*, and δ_A were based on long-term climatology weighted according to the monthly evaporative flux to appropriately simulate conditions occurring during the evaporation season when the isotopic enrichment signals are produced (see Gibson 2002). Note that atmospheric moisture is not assumed to be in isotopic equilibrium with precipitation, $\delta_A \neq \delta_P - \varepsilon^*$ but is calculated by coupled scaling of the δ_P–δ_P separation as a common fraction of ε^* for both ^2H and ^{18}O to achieve a best fit to the slope of the regional $\delta^{18}O$–δ^2H evaporative enrichment trend for all lakes. This approach, which accounts for departure from δ_A–δ_P isotopic equilibrium because of seasonality effects (J.J. Gibson, S.J. Birks, and T.W.D. Edwards, unpublished data), serves operationally to constrain δ_A, but sacrifices independent estimates of $\delta^{18}O$ and δ^2H. In this case, residual differences in the outputs from x estimates based on the individual tracers serve to bracket departures from the local evaporative enrichment trend. Importantly, it preserves a description of kinetic isotopic fractionation in the boundary layer that is consistent with established boundary layer theory (see Brutsaert 1982, pp. 91, 97). The isotopic composition of precipitation is estimated using Bowen and Revenaugh (2003), which is based on data from IAEAs Global Network for Isotopes in Precipitation (Birks et al. 2002).

Climate variables were estimated for each site from global gridded data sets (30 years, 1961–1990). Precipitation was estimated from the CRU 0.5 × 0.5 CL1.0 data set (New et al. 1999). E is calculated using a Hamon approach (Hamon 1961; New et al. 1999). Temperature and relative humidity were approximated based on the CRU 10-min climatology (New et al. 2002). The results from gridded climate data analysis indicate that lake surface evaporation (Hamon 1961; Kalnay et al. 1996) ranges from 391 to 462 mm, and precipitation ranges from 345 to 478 mm at study sites across the region. These numbers are in general agreement with other data sources for the region that report evaporation and precipitation numbers between 400 and 500 mm·year^{-1} (Environment Canada 1978). Latitude is also found to be inversely correlated with lake evaporation. For example, differences in evaporation rates are apparent between the southern sites in the Stony Mountains (average 449 mm) and sites in regions 5 and 6 (Caribou Mountains and Shield Lakes, averages 438 and 401 mm, respectively). Evaporation also exceeds precipitation (New et al. 1999) in this region by roughly 7%. Catchment areas for runoff production exceed lake areas by 89% on average. Transpiration is estimated to be 36%–50% of evaporation in this region (Abraham 1999), although landscape runoff presented herein are calculated from the isotope balance rather than using this value. Excluding groundwater inflows or recharge, climatological constraints suggest that water yield should be of the order of 25 to 200 mm·year^{-1} (Environment Canada 1978) across sites in the region, which as we show is less than the IMB-calculated range for the majority of lakes.

Water yield from IMB was calculated for the net catchment area of the 50 lakes using the x output results from eq. 3 and precipitation and evaporation over the lake (m^3) interpolated at each lake site:

$$(4) \qquad W_Y = \frac{E}{x} - P$$

where W_Y is the water yield (in mm·year^{-1}) estimated as W_Y·CA, where CA is net catchment area. Runoff ratio is estimated as the water yield from the catchment area divided by the precipitation volume on the catchment area. Residence time (τ, in years) of lake water was estimated as volume/inflow from the annual throughflow index (x), lake volume (V, m^3), and lake evaporation (E, m^3·year^{-1}), according to the method of Gibson et al. (2002):

$$(5) \qquad \tau = \frac{xV}{E} \quad \text{or} \quad \tau = \frac{V}{I}$$

The Water Survey of Canada (WSC) hydrometric estimates of water yield are based on available long-term average W_Y data (mm·year^{-1}) from 20 hydrometric gauging stations, grouped by representative watershed region (Fig. 3). The stations used in this analysis included both active and discontinued stations (65% and 35%, respectively). Most of the gauges (80%) are seasonally operated (March to October), whereas all of the continuous stations used for this analysis have been deactivated. WSC gauges are located some distance downstream but still within the broad-scale drainage areas of 20 lake sites. For 30 lakes, however, gauges located in adjacent or nearby watersheds were extrapolated to estimate water yield. Study lakes and their catchments in the Stony Mountains are illustrated (Fig. 3). WSC stations 07CD004 and 07CD004 are shown to illustrate the range in size of WSC catchments that may be used to represent water yield from this region. In general, WSC stations range in size from 54 to 14 300 km^2, and 67% of the basins applied in this study to calculate WSC water yield are less than 3000 km^2.

The study lakes are primarily headwater, as these sites are most likely to be sensitive to acid deposition. The location of lakes relatively high in watersheds means that none of the sites contains water survey gauges at its outlets. The lack of any direct measurements of inflow and outflow also preclude the calculation of water balance for comparison with IMB or the WSC water-yield estimates. The WSC hydrometric stations used in this study had an average collection record of 27 years, spanning the years 1962 to 2004. In cases where WSC gauges were operated for short periods of time (<10 years), the data were not considered reliable and were therefore not used.

Critical loadings (kequiv.H$^+$·ha^{-1}·year^{-1}) were approximated using the estimated W_Y (mm·year^{-1}) to represent the flux (mass × time) of the annual average net catchment runoff, according to (WRS 2004):

$$(6) \qquad CL_A = ([BC]_0 - [ANC_{lim}])\cdot W_Y \cdot 10^{-5}$$

where $[BC]_0$ is the nonmarine flux of base cation concentrations assumed to be equivalent to the sum of base cations in current lake water samples, W_Y equals runoff or water yield (mm·year^{-1}), and ANC_{lim} is the critical acid-neutralizing capacity limit, in this case, corresponding to a pH of 6.0 where

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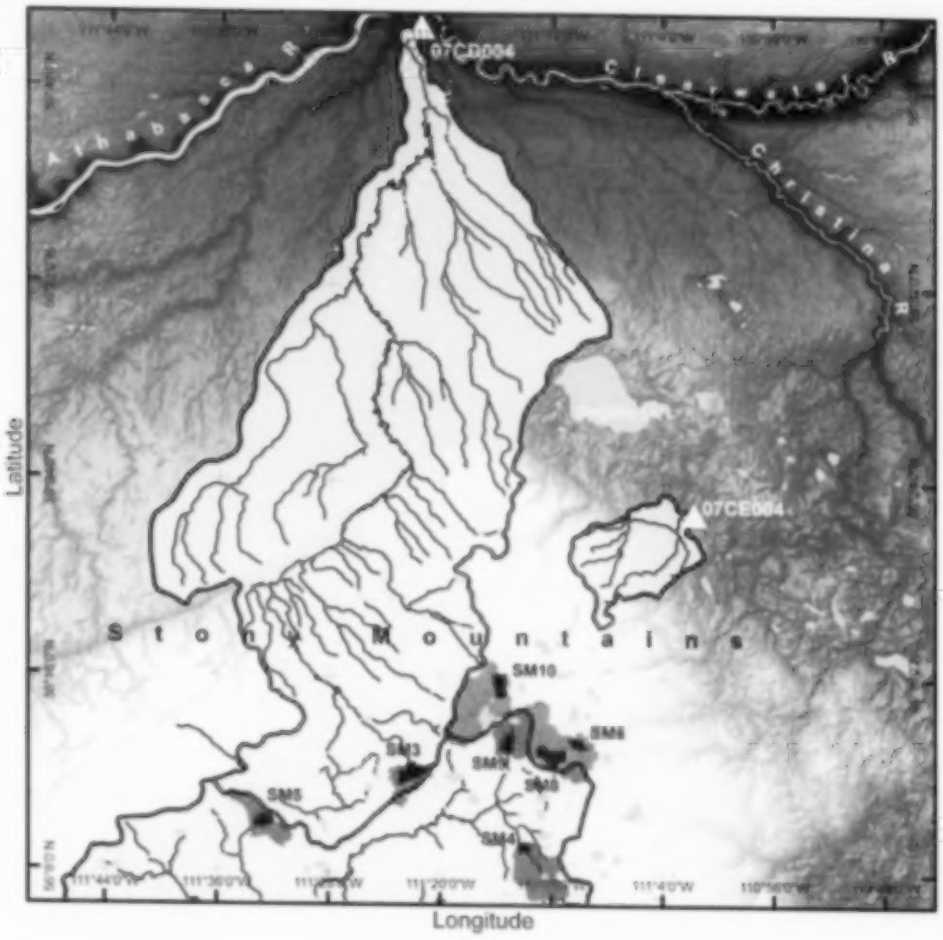
Fig. 3. Example of lake sites in the Stony Mountains and nearby Water Survey of Canada (WSC) gauges used to calculate the WSC water-yield estimate. Note that no lake sites have WSC gauges at their outlets.



biotic effects from acidification have been shown to occur (75 μequiv.·L^{-1} for all lakes; WRS 2004). The isotope mass balance model assumes that the lakes are operating at steady state and applies the use of water quality data from the late fall season, which is considered representative of annual average lake water chemistry (Henriksen et al. 1992; RAMP 2006). Bicarbonate is considered the primary buffering source for lakes, and surface runoff from the catchment is the only source of alkalinity (WRS 2004). Note that S4, originally part of the regional subset (n = 50), was not included in the critical acid loading analysis (n = 49) because data for $[BC]_0$ does not yet exist.

Exceedance occurs when the acid-generating processes are greater than the acid-buffering processes in lake systems. Exceedance is based on a potential acidifying input (PAI) scenario as described in WRS (2004), and the use of an exceedance measure enables us to comparatively examine affected aquatic features occurring within a region. The PAI scenario applied in this analysis uses a baseline assessment undertaken by Alberta Environment (Cheng et al. 1997). When CL_A is smaller than the PAI value, the lake is considered exceeded and therefore at risk of acidifying to a degree harmful to the biological indicator species. It is recognized that PAI values are approximate; however, predicted PAI values remain the primary indicator of acid deposition for accessing exceedance by industry (Imperial Oil 2005). PAI-based acid sensitivity estimates are included in this paper to illustrate the importance of accurate calculation of water yields for input into critical loadings estimates on which exceedance scenarios are built.

Results and discussion

Isotope systematics

As shown in this study (Fig. 4) and described in detail in previous boreal and arctic lakes surveys (Gibson et al. 1993, 2002, 2005), the systematic offset by evaporative isotopic enrichment from the meteoric water line (MWL) serves as a quantitative tracer of lake throughput (x) and, hence, as a flux-weighted measure of hydrological properties of the sur-

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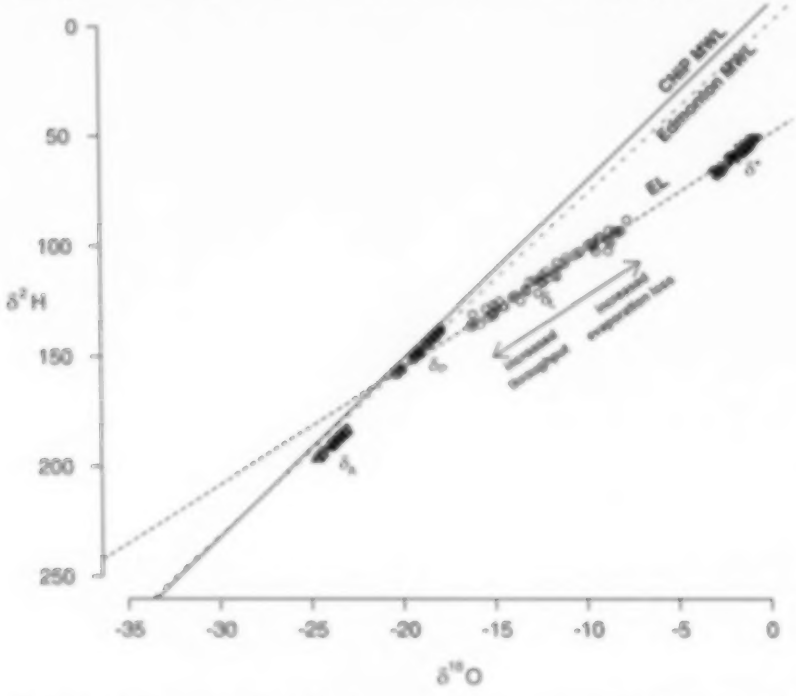
Fig. 4. δ^2H–$\delta^{18}O$ plot showing measured and modelled components of the isotope mass balance for the study lakes. MWL, meteoric water line based on Canadian Network for Isotopes in Precipitation ($\delta^2H = 7.8\delta^{18}O + 5.2$, $r^2 = 0.99$; Gibson et al. 2005); EL, evaporation line determined from regression of mean lake water δ_L values; δ_P are interpolated for latitude–longitude coordinates of each lake based on Bowen and Revenaugh (2003), and δ_A and δ^* are determined using a seasonal weighting algorithm described in the text.



rounding landscape. Both the Canadian Network for Isotopes in Precipitation (CNIP) MWL and the Edmonton CNIP MWL are illustrated; modelled isotopic compositions (δ_P; Bowen and Revenaugh 2003) fall close to the Edmonton CNIP MWL. Lakes that have lower inputs (precipitation + catchment yield) sit furthest away from the MWL towards the limiting isotopic enrichment, whereas lakes with higher input sit closer to the isotopic composition of precipitation. High water yielding lakes (Fig. 5*a*), for example, generally exhibit isotopic lake water signatures δ_L of approximately –14 to –16 $\delta^{18}O‰$ and have increased throughput, whereas low water yield systems exhibit isotopic signatures around the range of –7 to –9 $\delta^{18}O‰$ and have increased evaporation loss (quantitative results and comparisons are presented in Table 4 and illustrated in Figs. 5 and 6).

Hydrologic indicators

The fraction of water loss by evaporation (x, eq. 3) is shown to span the continuum between 8% and 75%, suggesting considerable range in the hydrologic conditions of lakes in the region; lakes with highest x values function as precipitation-fed basins with minor runoff from surrounding areas, whereas those with lowest x values function as nodes in the regional river drainage network, with rapid surface water – groundwater throughput. Residence time (eq. 5) of water in the lakes is also highly variable (~0.2–7 years) and is weakly correlated ($r^2 = 0.24$) with water yield, as residency depends on x and volume, or water yield and volume. Average differences between ^2H and ^{18}O estimates of water yield (eq. 4) are –3% (±3%), which is a useful measure of uncertainty using the best-fit approach as applied with $\delta_P - \delta_A = 0.72\varepsilon^*$ (70% of liquid–vapour equilibrium separation). Year-to-year fluctuations measured in ^{18}O water yield range from 96 to 118 mm·year^{-1}, a difference from the composite water yield (3-year) estimate of –8%, 11%, and –10% in 2002, 2003, and 2004, respectively.

Water yield (W_Y, eq. 4), which is effectively calculated from the IMB by subtracting the influence of direct precipitation falling on the lake, is predicted to be in the range of 4×10^4 to 5×10^6 m^3·year^{-1}. The depth-equivalent IMB W_Y, which accounts for catchment area, ranges from 5–395 mm·year^{-1} compared with 23–196 mm·year^{-1} estimated based on interpolation of stream flow (WSC) data. Differences between the years of study and the long-term climate and hydrology (Table 2) are not anticipated to create large errors in estimate of IMB water yield; even through summers were warmer and drier in general during the study years, only a small difference in runoff was observed. A comparison of the results of IMB and WSC are shown (Fig. 5*a*), where precipitation and evaporation estimates are provided for each lake based on 1961–1990 climate normal (Fig 5*b*). Note that W_Y results are ordered according to the IMB–WSC offset (by percent fraction of IMB) to emphasize the systematic similarities and differences between the two approaches. It is encouraging to note that average water yields of close to 110 mm·year^{-1} (±6 mm·year^{-1}) were obtained for both methods, although median values were 33% lower for IMB, as discussed later in the paper.

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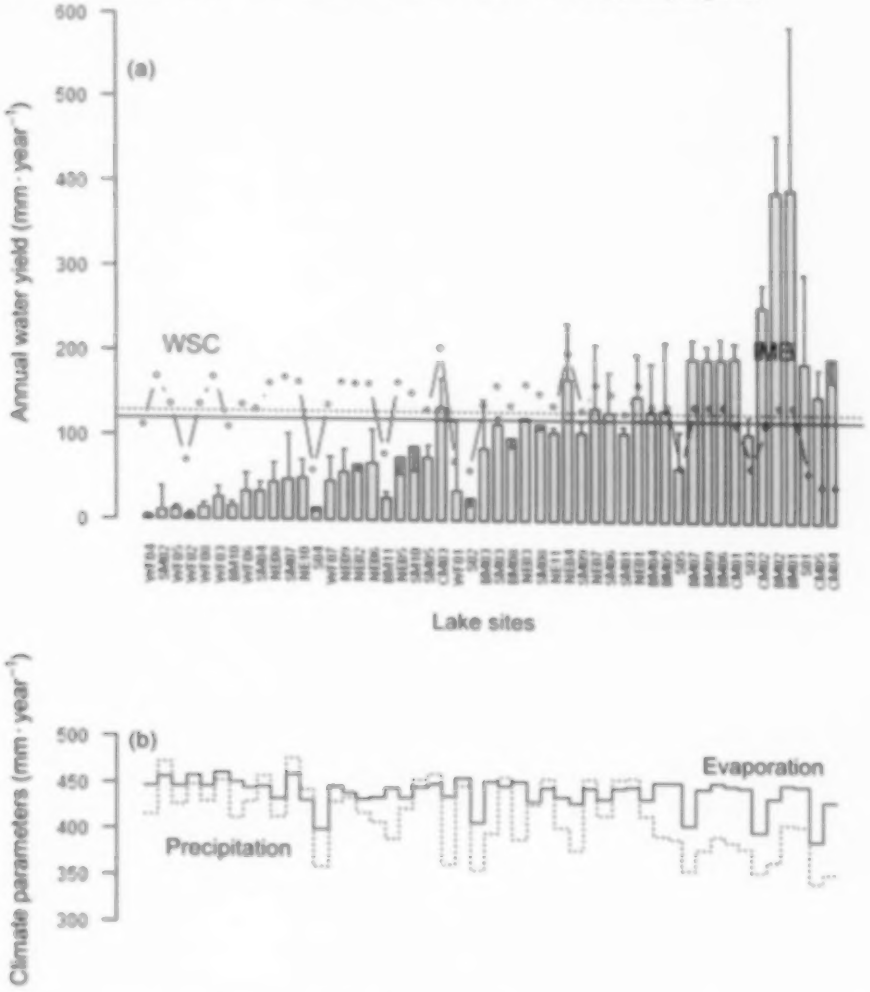
Fig. 5. Plot of water yield (W_Y) and interpolated climate fields for various lakes depicting the hydrologic "pulse" of the systems. (*a*) W_Y results for IMB (isotope mass balance model; bars) and WSC (Water Survey of Canada; open circles) are sorted by the fractional differences between the two estimates (IMB – WSC). Error bars illustrate the standard deviations for IMB water yields. The dotted line is average WSC W_Y; the solid line is average IMB W_Y, similar for both methods. (*b*) Climate parameters: precipitation (P) is shown as a dotted line; evaporation (E) is shown as a solid line. Note that $P - E$ is typically negative.



Upon closer examination, three distinct populations of lakes can be identified (Fig. 5*a*) comprising lakes in which WSC W_Y estimates were greater than ±50% of IMB and lakes in which the two estimates of water yield were within reasonable bounds (WSC fraction of IMB < 50%, 24 lakes). Lake systems (19) in which WSC W_Y was higher than IMB W_Y (Fig. 5*a*) by 50% tended to have smaller surface areas (60% below that of the data set average) and were located primarily in low-elevation boreal plain environments (regions 1 and 3). Possible errors in the IMB such as non-steady-state conditions within these small lakes or pre-enrichment owing to evaporative waters entering into lakes are likely causes of some, but not all, of the differences between the two methods (Fig 6*b*). At the other end of the spectrum, WSC W_Y is lower than IMB W_Y at seven lakes, four of which are large, deep lake systems (lake surface areas more than 500% greater than the data set average); these lakes are discussed in more detail later in the paper. Removing the effect of the very small and very large systems results in observed values (25th and 75th percentiles) in IMB water yield estimates ranging from 39 to 135 mm·year^{-1}, whereas WSC estimates range from 100 to 150 mm·year^{-1}. The IMB estimate of water yield is directly comparable with known observations (Environment Canada 1978) of runoff for the region, noted earlier in the paper, whereas the WSC fails to capture the low range of water yields. The observed pattern is reasonable considering that WSC W_Y is a large-scale, interpolated estimate, whereas IMB is based on fine-scale, site-specific conditions, which more closely resemble the variability of lake sizes and landscapes present in this complex region (RAMP 2006).

Unfortunately, because of difficulty in gauging lake outflows in the region, it was not possible to directly compare IMB and WSC estimates for identical lake-drainage areas

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Table 4. Comparison of hydrologic indices and their potential impact on aquatic loadings and exceedance status.

	Isotope mass balance									Hydrometric			Critical loadings status	
Lake no.	x $\delta^{18}O$ (‰)	Diff. x from δ^2H (‰)	Residence time (year)	IMB W_Y ($m^3 \cdot year^{-1}$)	IMB W_Y ($mm \cdot year^{-1}$)	IMB 2002 W_Y ($mm \cdot year^{-1}$)	IMB 2003 W_Y ($mm \cdot year^{-1}$)	IMB 2004 W_Y ($mm \cdot year^{-1}$)	IMB runoff ratio	WSC W_Y ($m^3 \cdot year^{-1}$)	WSC W_Y ($mm \cdot year^{-1}$)	WSC runoff ratio	IMB CL_A (kequiv. $H^+ \cdot ha^{-1} \cdot year^{-1}$)	Exceedance condition
NE1	12.7	–0.7	0.35	1 957 900	149	230	166	114	0.36	1 968 600	150	0.36	0.25	Same
NE2	11.4	–1.0	0.33	1 141 000	67	119	64	47	0.16	2 550 500	150	0.36	0.18	Same
NE3	15.9	2.2	0.23	2 700 500	169	200	161	145	0.45	3 061 100	192	0.51	0.56	Same
NE4	23.7	–2.5	0.79	811 300	122	112	135	114	0.29	996 200	150	0.35	0.52	Changed
NE5	36.0	–0.3	0.75	1 491 100	76	61	94	70	0.18	2 987 200	153	0.36	0.49	Same
NE6	18.3	0.8	0.37	735 800	69	106	79	50	0.17	1 603 900	150	0.37	0.25	Same
NE7	8.1	–1.5	0.19	551 000	135	218	122	100	0.32	611 600	150	0.36	0.31	Same
NE8	14.4	–1.0	0.27	298 000	46	75	47	30	0.11	971 500	150	0.36	0.15	Changed
NE9	54.5	–5.9	1.38	1 173 500	58	46	63	60	0.13	3 066 100	153	0.35	0.92	Same
NE10	55.1	–4.9	0.98	1 423 800	51	33	34	65	0.12	4 222 800	153	0.34	0.66	Same
NE11	26.0	0.8	0.79	7 353 000	107	–41	119	96	0.26	8 474 600	123	0.30	2.02	Same
SM1	57.5	–3.7	0.86	758 600	107	73	105	131	0.23	807 800	114	0.25	0.57	Same
SM2	75.0	–4.0	0.94	269 500	11	1	7	23	0.02	3 850 000	158	0.34	0.03	Changed
SM3	47.9	–2.9	1.55	888 400	116	94	126	110	0.25	1 141 900	149	0.32	0.13	Same
SM4	36.1	–2.8	0.57	410 800	34	21	48	35	0.07	1 418 400	118	0.26	0.04	Same
SM5	49.5	–2.6	1.27	473 300	75	74	74	70	0.16	743 800	118	0.26	0.05	Same
SM6	41.0	–1.5	0.81	441 500	130	110	128	143	0.28	474 200	140	0.31	0.35	Same
SM7	68.3	6.6	1.90	285 600	49	8	58	83	0.10	916 400	158	0.33	0.08	Same
SM8	43.0	–1.3	0.85	1 114 700	115	84	115	121	0.25	1 358 100	140	0.31	0.04	Same
SM9	32.2	–3.1	0.41	999 600	106	104	108	103	0.23	1 119 600	118	0.26	0.04	Same
SM10	28.2	–1.3	0.44	1 523 500	88	82	84	87	0.19	2 429 800	140	0.31	0.09	Changed
WF1	63.1	5.6	0.81	883 200	36	4	46	45	0.08	1 269 700	52	0.12	0.23	Same
WF2	70.8	5.3	1.45	150 000	6	1	10	7	0.01	1 225 500	52	0.12	0.00	Same
WF3	48.7	3.9	1.02	1 071 600	28	13	29	44	0.06	6 045 000	158	0.35	0.07	Changed
WF4	64.0	15.4	1.20	9 700	5	5	4	5	0.01	173 800	97	0.23	0.07	Changed
WF5	54.2	7.0	0.91	93 100	14	6	18	13	0.03	855 700	124	0.29	0.09	Changed
WF6	31.6	4.3	0.69	177 700	35	17	53	40	0.08	636 300	124	0.29	0.13	Changed
WF7	32.5	0.8	0.58	80 300	47	25	83	42	0.11	212 700	124	0.29	0.38	Same
WF8	69.2	–3.0	1.11	437 700	16	7	21	17	0.04	3 363 700	124	0.29	0.11	Changed
BM1	28.2	–3.1	3.61	20 250 200	395	345	444	375	0.97	6 367 400	124	0.30	0.60	Same
BM2	30.6	–3.5	7.01	46 862 500	392	345	445	365	0.96	14 844 700	124	0.30	1.61	Same
BM3	15.2	1.6	0.46	2 488 600	87	65	114	69	0.22	3 551 200	124	0.31	0.42	Same
BM4	31.3	1.1	0.30	4 490 100	132	131	182	86	0.33	4 230 700	124	0.31	0.48	Same
BM5	25.3	0.3	0.25	3 700 300	133	117	199	90	0.34	3 460 800	124	0.32	0.65	Same
BM6	14.3	1.2	0.16	3 568 400	194	213	235	142	0.50	2 282 700	124	0.32	0.23	Same
BM7	17.1	–2.3	0.25	1 506 100	193	173	176	205	0.51	969 300	124	0.33	0.03	Same
BM8	14.8	1.2	0.37	3 239 300	99	99	126	76	0.25	4 055 300	124	0.32	0.34	Same
BM9	21.9	–1.4	1.55	5 835 900	193	151	232	194	0.49	3 754 700	124	0.31	0.14	Same
BM10	70.9	6.6	0.58	88 000	17	19	16	14	0.04	486 300	95	0.23	0.17	Same
BM11	38.5	1.9	0.21	42 100	28	20	33	32	0.07	90 200	61	0.16	0.06	Same

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Table 4 (*concluded*).

	Isotope mass balance			Hydrometric							Critical loadings status	
Lake no.	x $\delta^{18}O$ (‰)	Diff. x from δ^2H (‰)	Residence time (year)	IMB W_Y (m^3·year^{-1})	IMB W_Y (mm·year^{-1})	IMB 2002 W_Y (mm·year^{-1})	IMB 2003 W_Y (mm·year^{-1})	IMB 2004 W_Y (mm·year^{-1})	IMB runoff ratio	WSC W_Y (m^3·year^{-1})	WSC W_Y (mm·year^{-1})	WSC runoff ratio	IMB CL_A (keq·H$^+$·ha^{-1}·year^{-1})	Exceedance condition
CM1	13.5	−1.9	1.95	4 693 900	196	178	228	184	0.51	2 382 400	100	0.26	0.75	Same
CM2	31.5	−6.0	2.06	9 722 900	256	260	283	213	0.70	3 775 200	100	0.27	0.93	Same
CM3	23.8	−2.4	0.95	3 385 600	134	163	139	102	0.37	4 955 400	196	0.54	0.03	Same
CM4	14.4	−1.9	2.75	6 978 800	195	195	214	163	0.55	805 800	22	0.06	0.65	Same
CM5	41.1	−5.2	1.49	386 300	130	174	165	106	0.42	57 900	22	0.06	0.26	Same
S1	35.8	−3.9	6.04	2 545 900	180	176	220	163	0.55	533 100	40	0.12	0.8	Same
S2	12.2	1.4	1.05	3 073 600	28	25	30	28	0.08	4 386 900	40	0.11	0.14	Same
S3	15.8	0.9	1.31	3 170 500	107	83	121	105	0.30	1 392 400	47	0.13	0.39	Same
S4	24.2	2.3	2.41	1 835 900	15	12	18	15	0.04	4 896 900	40	0.11	N/A	N/A
S5	31.6	4.3	0.77	295 200	66	60	70	66	0.18	210 000	47	0.13	0.32	Same

Notes: See eq. 3 for x; Diff. x from δ^2H, the difference between x calculated from $\delta^{18}O$ and x calculated from δ^2H; W_Y, catchment water yield; IMB, isotope mass balance model; WSC, Water Survey of Canada; CL_A, critical acid loads.

without interpolation. Nor is it possible at the present time to apply IMB directly at the WSC river gauging stations. Without the benefit of a flux-weighted reservoir δ_L, estimation of the isotopic composition of discharge δ_Q in eq. 2 for a river outlet requires a multiyear time-series isotope record, which is currently unavailable at the sites in the area. Error ranges for the IMB and WSC models can be gleaned from ranges in the standard deviations for measured data and the differences in the 2002–2004 modelled water yields (Table 4). Water yield is measured for both IMB and WSC; W_Y from the WSC gauges is measured in the field over a 43-year period, and isotope measurements are sampled at lake sites over a 3-year period. All other parameters used to calculate the IMB and WSC W_Y estimates are applied to both models equally. The IMB W_Y estimates (based on ±1 SD in $\delta^{18}O$ measured at the lakes) range from 94 to 132 mm·year^{-1}, whereas the WSC W_Y estimates, calculated as ±1 SD in the gauge runoff, range from 53 to 179 mm·year^{-1}. Hence, although the range in the W_Y estimates as provided by IMB was larger than that of the WSC, the variability (as calculated using ±1 SD) across isotopic estimates was lower than that of the gauged runoff.

To determine the range in W_Y estimates obtained over the three study years, water yields were calculated for each individual year. Note that the IMB model estimates provided as comparison to WSC estimates are based on the average signal over the 3-year period of 2002–2004 (Table 4, WSC yearly data not shown). Both estimates of water yield respond, on a relative basis, similarly to average variations in climate; however, the IMB W_Y mirrors the contributions of average precipitation throughout the 3 years. For example, rainfall + snowfall is greatest in 2002 and 2003 and least in 2004, which is reflected in the average IMB results (data not shown). Temperature variations, on the other hand, reflect the WSC estimate; for example, maximum temperatures were greatest in 2003 and lowest in 2002. Further analysis of the combined effects of climate on water yields at more appropriate temporal scales is required to fully understand these relationships.

As noted previously, the median W_Y values were 33% lower for IMB than WSC. This is largely attributed to elevated IMB W_Y for several large, deep lakes (CM2, S1, BM1, and BM2), which were suspected of being connected to regional groundwater flow systems. The uniqueness of these lakes is apparent when examining the average lake area and maximum depth, which are 18.5 km^2 and 17.5 m, respectively, for the four lakes compared with the survey averages of 3 km^2 and 4.3 m, respectively. Similar lakes displaying elevated runoff ratios have been reported in previous isotopic surveys on the boreal plain (Gibson et al. 2005). Because of their increased volume, these lakes also tended to have longer residence times (eq. 5), despite greater water yields. Volumetric runoff ratios (W_Y/P) were also calculated to evaluate whether the watersheds could plausibly sustain the estimated water yields. Typically, runoff ratios range from 0.1 to 0.5 for precipitation-fed systems in the area, but potentially higher values for groundwater-fed systems, especially fens, might arise (Gibson et al. 2005). For the study lakes in general, runoff ratios were found to range from 0.01 to 0.97 for IMB compared with 0.06 and 0.54 for the WSC approach. The upper limit of the IMB runoff ratio decreases from 0.97

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to 0.55 when the large, deep lakes are excluded from the analysis. Although groundwater originating from outside the topographic catchment area is the most likely hypothesis for elevated water yields and runoff ratios in these deep lakes, other uncertainties were also considered. Errors associated with drainage basin area delineation, a problem common in low-relief wetland-rich areas, were judged to be unlikely as the lakes are found in relatively incised terrain. Furthermore, a threefold increase in watershed area would be required in all cases to account for the "excess" water. Chain-of-lake effects (Gat and Bowser 1991) were also considered because the problematic systems are large, non-headwater systems with many contributing lakes feeding into them. However, this effect would in fact result in lower water yields as preenrichment of heavy isotopes would accentuate apparent evaporation losses from the system.

As presented, IMB estimates are a first approximation of the water-yield conditions across the 50-lake survey. These estimates should be regarded as guidelines that may be refined over time as monitoring and sampling continue at the sites. Nevertheless, the estimates serve to demonstrate the difference between use of site-specific and regionally interpolated estimates of water yield, a difference that helps to illustrate the potential improvements from incorporation of site-specific IMB into critical loadings assessments.

Critical loadings comparison

Critical loads of acidity CL_A for the study sites are presented for each method (Fig. 6*a*, where the order of lakes from Fig. 5 is preserved), and IMB critical acid loading estimates are also presented (Table 4). Note that the lake number is reduced from 50 to 49 for CL_A calculations as one lake (S4) had insufficient data for calculation of the measure. CL_A is also compared with a preliminary potential acid input (PAI) scenario for the region described in WRS (2004), whereby lakes with CL_A > PAI are considered to be potentially sensitive to acidification (Fig. 6*a*). Despite the first-order nature of the PAI and CL_A models and underlying data sets noted earlier, these provide a practical basis for comparing the propagation of W_Y effects on the assessment. Differences between the IMB and WSC versions are further illustrated (Fig. 6*b*), highlighting lakes for which exceedance status changes when the site-specific IMB results are applied (see also Table 4). In total, exceedance status based on IMB was different in nine of the 49 lakes (18%; Table 4), eight of which were identified as being potentially exceeded as a result of acid inputs and one switched to not-exceeded status. Elevated sensitivity was due to a lower water yield calculated by the IMB method. The one lake (BM07) with reduced sensitivity had elevated water yield calculated by the IMB method and therefore a higher annual loading of base cations (see RAMP (2006) for chemistry data). Differences in CL_A at both extremes of the hydrologic spectrum are nevertheless considerable even for lakes where exceedance status does not change (Figs. 6*a* and 6*b*).

Regionally, changes in exceedance status only appear to affect lakes in the northeast Fort McMurray, Stony Mountains, and west Fort McMurray regions, where PAI is more likely to be close to CL_A, and not in the more distant Birch Mountains, Caribou Mountains, and Shield Lakes regions, despite presence of low-yield systems in all. Improvements in these preliminary assessments will require better characterization of the chemistry of runoff and its variability, as well as improved representation of peatland characteristics.

Lake and watershed characteristics

To further understand under what conditions WSC-based water yields were similar to those of IMB, a comparison was made of lake and watershed characteristics for sites with similar W_Y and within the zone of agreement (<50% IMB–WSC, shown in Fig. 5*a*). This coarse-scale analysis sheds some light on landscape controls at work across this region of the boreal forest; however, results would be greatly improved through the application of finer-scale data sets, region by region across the study area. Similarities between the study watersheds and the large WSC basins were evaluated from regression analysis that included factors such as drainage basin area, catchment elevation, slope, and drainage ratio, and vegetation characteristics such as percent coverage of fen, bog, and upland were compared where data permitted. Initial results suggest that differences in WSC and IMB estimates of W_Y are more similar when the slope and elevation of the study watershed are similar to those of the larger WSC watershed, when the slope is higher, and when water residence times in the lakes are comparatively short. Disconnected behaviour of some low- and high-throughput lakes apparently connected to regional groundwater was not captured by the WSC network, which tended to represent mean conditions. Fen area and bog area (at sites where wetlands comprised greater than 50% of the catchment area) were also found to be comparatively important controls on water-yield differences in the systems (r^2 = 0.17 and 0.16, p < 0.05, for fens and bogs, respectively), although the very coarse-scale data sets used to analyse wetlands are not considered sufficient to illustrate this relationship. Additionally, the low water yield regions such as regions 1 and 3 are anticipated to have high percentage wetland and deeper surficial materials (see Smerdon et al. (2007) for a discussion of the influence of depth of surficial materials in a study site slightly further south of these regions), which control water movement across these landscapes; however, relationships could not be found given the existing data. WSC estimates are also improved when IMB lake sites are situated within the broader-scale WSC catchment, illustrating the importance of consistent landscape controls between interpolated sites. Increased density of a gauging network might be one approach to improve hydrologic calculations. Such enhancements seem unlikely considering the movement towards divestment in government-sponsored monitoring in recent years (Shiklomanov et al. 2002).

Research implications

Water yield is often the most unreliable parameter in critical load calculations. Commonly, water yield is based solely on estimates from the available hydrometric network. This study demonstrates an alternative method for estimating site-specific water yield to lakes based on isotope mass balance, applies the approach to calculate water yield and critical acid loadings for 49 lakes in northeastern Alberta, and compares the results with a conventional hydrometric interpolation approach. Importantly, the results suggest that the hydrometric networks fail to capture the scale-dependant

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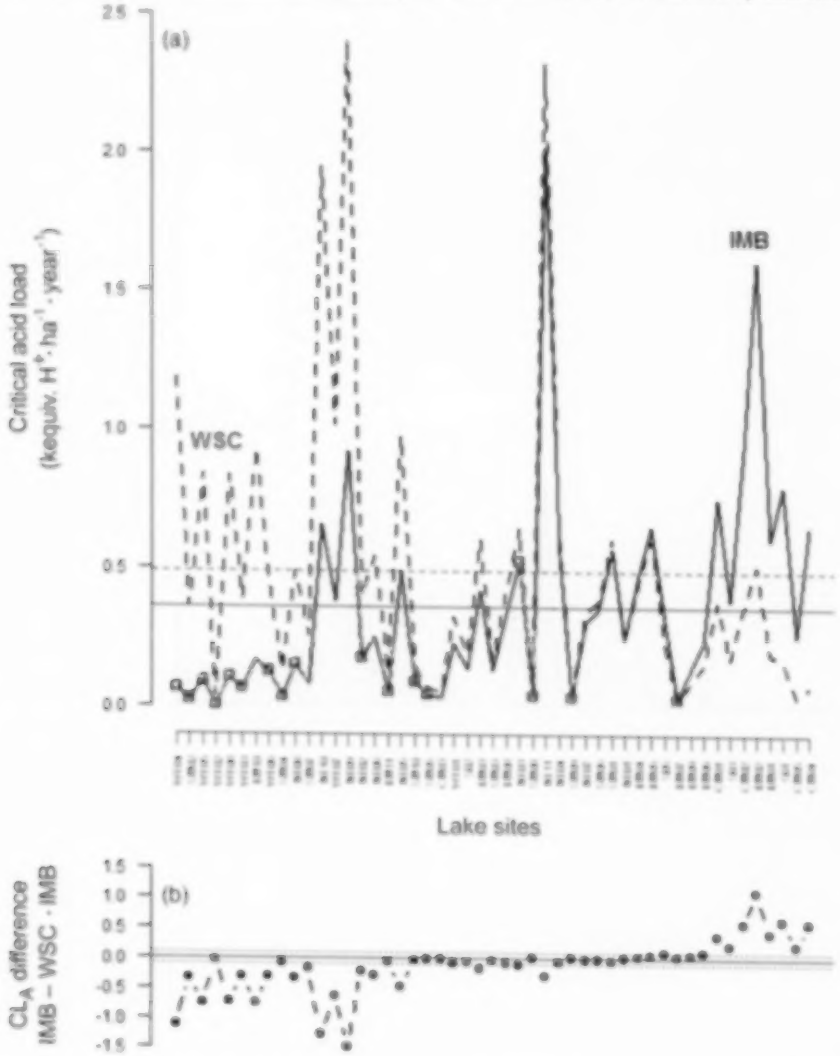
Fig. 6. (*a*) Pulse diagram illustrating a preliminary critical acid loadings (CL_A) scenario for study sites based on isotope mass balance (IMB; solid line) and Water Survey of Canada (WSC; broken line) water yields (W_Y). The shaded hatched background represents the potential acidifying input (PAI) value for each study site. When the PAI value is greater than the critical load, sites are considered acid-sensitive (exceeded systems are illustrated by a square). (*b*) Pulse diagram illustrating difference in predicted critical loads associated with use of in situ IMB W_Y versus interpolated WSC W_Y. Lakes where exceedance conditions depend on W_Y method used are indicated by solid circles.



hydrologic variability present within the boreal landscapes, particularly in some of the most sensitive systems such as the small, evaporative lakes with low runoff. To our knowledge, this is the first time that a critical loadings assessment has been refined using measurements of the stable isotopes of water.

The hydrologic conditions observed (IMB) at study lakes are directly comparable with those of previous studies in the region (Environment Canada 1978; Prepas et al. 2001; Gibson et al. 2002). Four lakes that were found to have high water yields are situated in the Caribou and Birch mountains, zones of enhanced regional groundwater flow, and may reflect deep regional groundwater inputs occurring outside topographically defined local catchments (Toth 1963; Winter et al. 2003). The analysis also reinforces past observations that the boreal plain is in general characterized by a net water deficit (Winter 1989; Ferone and Devito 2004), i.e., evaporation generally exceeds precipitation, so that most lakes depend on runoff from the catchment or groundwater inputs to maintain a long-term hydrologic balance.

The low threshold of evaporative lakes to acidification is important to realize. In Alberta's boreal region of Canada, despite strident controls on emissions, lakes are at high risk to acid deposition because the extent and severity of current impacts is unknown. Small lakes, which comprise a greater percentage of the lake systems of the boreal landscape, are primarily impacted by approaches to calculating sensitive model parameters such as water yield. One promising aspect

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is that the identification of lakes at risk is possible using the stable isotopes of water, which are easily incorporated into water quality surveys and may help to elucidate aquatic systems at risk at the regional, national, and continental scale.

Collaborative studies are also currently underway to incorporate a refined version of the IMB into a dynamic critical loadings assessment for the region using a model similar to MAGIC (Model of Acidification of Groundwater in Catchments) (see Aherne et al. 2003).

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References

Abraham, C. 1999. Evaporation and evapotranspiration in Alberta. Alberta Environmental Protection, Water Sciences Branch, Water Management Division, Edmonton, Alberta.

Aherne, J., Dillon, P.J., and Cosby, B.J. 2003. Acidification and recovery of aquatic ecosystems in south-central Ontario, Canada: regional application of the MAGIC model. Hydrol. Earth Sys. Sci. **7**(4): 561–73.

Birks, S.J., Gibson, J.J., Gourcy, L., Aggarwal, P.K., and Edwards, T.W.D. 2002. Maps and animations offer new opportunities for studying the global water cycle. EOS, **83**(37): September 2002 + electronic supplement http://www.agu.org/eos_elec/eeshome.html.

Bothe, R.A., and Abraham, C. 1987. Evaporation and evapotranspiration in Alberta: 1912 to 1985. Alberta Environment, Technical Services Division, Hydrology Branch, Edmonton, Alberta.

Bothe, R.A., and Abraham, C. 1993. Evaporation and evapotranspiration in Alberta: 1986 to 1992. Addendum. Alberta Environment, Technical Services Division, Hydrology Branch, Edmonton, Alberta.

Bowen, G.J., and Revenaugh, J. 2003. Interpolating the isotopic composition of modern meteoric precipitation. Water Resour. Res. **39**(10): 1299, doi:10.1029/2003WR002086.

Brown, J., Ferrians, O.J., Jr., Heginbottom, J.A., and Melnikov, E.S. 1998. Circum-Arctic map of permafrost and ground-ice conditions [revised February 2001]. National Snow and Ice Data Center/World Data Center for Glaciology, Boulder, Colorado. Digital media.

Brutsaert, W. 1982. Evaporation into the atmosphere: theory, history and applications. D. Reidel Publishing Co., Boston, Mass. pp. 91–97.

Cheng, L., McDonald, K., Fox, D., and Angle, R. 1997. Total potential acid input in Alberta. Alberta Environmental Protection, Edmonton, Alberta.

Coplen, T.B. 1996. New guidelines for reporting stable hydrogen, carbon, and oxygen isotope-ratio data. Geochim. Cosmochim. Acta, **60**: 3359–3360.

Environment Canada. 1978. Hydrological atlas of Canada. Canadian National Committee for the International Hydrological Decade, Fisheries and Environment Canada, Ottawa, Ontario.

Erickson, P.K. 1987. An assessment of the potential sensitivity of Alberta lakes to acid deposition. Water Quality Control Branch, Alberta Environment, Edmonton, Alberta.

Ferone, J.M., and Devito, K.J. 2004. Shallow groundwater – surface water interactions in pond–peatland complexes along a Boreal Plains topographic gradient. J. Hydrol. **292**(1–4): 75–95.

Fulton, R.J. 1996. Surficial material map of Canada — map 1880A, scale 1 : 5 000 000. Natural Resources Canada, Terrain Sciences Division, Ottawa, Ontario.

Gat, J.R. 1995. Stable isotopes of fresh and saline lakes. *In* Physics and chemistry of lakes. *Edited by* A. Lerman, D. Imboden, and J. Gat. Springer-Verlag, New York. pp. 139–166.

Gat, J.R. 1996. Oxygen and hydrogen isotopes in the hydrological cycle. Annu. Rev. Earth Planet. Sci. **24**: 225–262.

Gat, J.R., and Bowser, C.J. 1991. Heavy isotope enrichment in coupled evaporative systems. *In* Stable isotope geochemistry: a tribute to Samuel Epstein. Lancaster Press, San Antonio, Texas. pp. 159–168.

Gibson, J.J. 2002. A new conceptual model for predicting isotopic enrichment of lakes in seasonal climates. PAGES News, **10**: 10–11.

Gibson, J.J., Edwards, T.W.D., Bursey, G.G., and Prowse, T.D. 1993. Estimating evaporation using stable isotopes: quantitative results and sensitivity analysis for two catchments in northern Canada. Nord. Hydrol. **24**: 79–94.

Gibson, J.J., Prepas, E.E., and McEachern, P. 2002. Quantitative comparison of lake throughflow, residency, and catchment runoff using stable isotopes: modelling and results from a regional survey of boreal lakes. J. Hydrol. **251**: 1–13.

Gibson, J.J., Edwards, T.W.D., Birks, S.J., St. Amour, N.A., Buhay, W., McEachern, P., Wolfe, B.B., and Peters, D.L. 2005. Progress in isotope tracer hydrology in Canada. Hydrol. Process. **19**: 303–327.

Gonfiantini, R. 1986. Environmental isotopes in lake studies. *In* Handbook of environmental isotope geochemistry. *Edited by* P. Fritz and J.C. Fontes. Elsevier, New York. pp. 113–168.

Hamon, W.R. 1961. Estimating potential evapotranspiration. J. Hydraul. Div., Proc. Am. Soc. Civil Eng. **87**: 107–120.

Henriksen, A., Kämäri J., Posch, M., and Wilander, A. 1992. Critical loads of acidity: Nordic surface waters. Ambio, **21**: 356–363.

Horita, J., and Wesolowski, D.J. 1994. Liquid–vapor fractionation of oxygen and hydrogen isotopes of water from the freezing to the critical temperature. Geochim. Cosmochim. Acta, **58**: 3425–3437.

Imperial Oil. 2005. Kearl Lake Environmental Impact Assessment. Vol. 5. Air and noise — air quality. Imperial Oil Resources Ltd., Calgary, Alberta, Canada.

Kalnay, E., Kanamitsu, M., Kistler, R., Collins, W., Deaven, D., Gandin, L., Iredell, M., Saha, S., White, G., Woollen, J., Zhu, Y., Leetmaa, A., Reynolds, R., Chelliah, M., Ebisuzaki, W., Higgins, W., Janowiak, J., Mo, K.C., Ropelewski, C., Wang, J., Jenne, R., and Joseph, D. 1996. The NCEP/NCAR 40-Year Reanalysis Project. Bull. Am. Meteorol. Soc. **77**(3): 437–471.

Merlivat, L., and Coantic, M. 1975. Study of mass transfer at the air–water interface by an isotopic method. J. Geophys. Res. **80**: 3455–3464.

Meteorological Service of Canada. 2004. National climate data archive of Canada. Meteorological Service of Canada, Environment Canada, Doval, Quebec.

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New, M., Hulme M., and Jones, P. 1999. Representing twentieth-century space–time climate variability. Part II. Development of 1901–96 monthly grids of terrestrial surface climate. J. Clim. **13**: 2217–2238.

New, M., Lister, D., Hulme, M., and Makin, I. 2002. A high-resolution data set of surface climate over global land areas. Clim. Res. **21**: 1–25.

Prepas, E.E., Plana, D., Gibson, J.J., Vitt, D.H., Prowse, T.D., Dinsmore, L.A., Halsey, P.M., McEachern, P.M., Paquet, S., Scrimgeour, G.J., Tonn, W.M., Paszkowski, C.A., and Wolfstein, K. 2001. Landscape variables influencing nutrients and phytoplankton communities in Boreal Plain lakes of northern Alberta: a comparison of wetland- and upland-dominated catchments. Can. J. Fish. Aquat. Sci. **58**: 1286–1299.

Regional Aquatics Monitoring Program. 2004. 2003 technical report to the Regional Aquatics Monitoring Program. Appendix A8: acid sensitive lakes. http://www.ramp-alberta.org/archive.php.

Regional Aquatics Monitoring Program. 2006. 2005 technical report to the Regional Aquatics Monitoring Program. Appendix A8: acid sensitive lakes. http://www.ramp-alberta.org/archive.php.

Schindler, D.G. 1996. The response of aquatic systems in Alberta to acidifying emissions. *In* Scientific appendix to the final report of the Target Loading Subgroup on Critical and Target Loading in Alberta. Clean Air Strategic Alliance, Edmonton, Alberta.

Shields, J.A., Tarnocai, C., Valentine, K.W.G., and MacDonald, K.B. 1991. Soil landscapes of Canada: procedures manual and user's handbook. Land Resource Research Centre, Research Branch, Agriculture Canada, Ottawa, Ont.

Shiklomanov, A.I., Lammers, R.B., and Vorosmarty, C.J. 2002. Widespread decline in hydrological monitoring threatens pan-Arctic research. AGU Eos Trans. **83**(13): 16–17.

Smerdon, B.D., Mendoza, C.A., and Devito, K.J. 2007. Similations of fully coupled lake–groundwater exchange in a subhumid climate with an integrated hydrologic model. Water Resour. Res. **43**: W01416, doi:10.1029/2006WR005137.

Soil Landscapes of Canada Working Group. 2005. Soil landscapes of Canada. Version 3.0. Agriculture and Agri-Food Canada, Digital map and database at 1:1 million scale. http://sis.agr.gc.ca/cansis/nsdb/slc/v3.0/intro.html.

Toews, M.W., Whitfield, P.H., and Allen, D.A. 2007. Seasonal statistics: the 'seas' package for R. Comput. Geosci. **33**(7): 944–951.

Toth, J. 1963. A theoretical analysis of groundwater flow in small drainage basins. J. Geophys. Res. **68**: 4795–4812.

Vitt, D.H., Halsey, L.A., Thormann, M.N., and Martin, T. 1996. Peatland inventory of Alberta. Phase 1. Overview of peatland resources in the natural regions and subregions of the province. Forestry, Lands and Wildlife Maps, Edmonton, Alberta.

Western Resource Solutions. 2004. Calculation of critical loads of acidity to lakes in the Athabasca Oil Sands Region. Report to the NOx SOx Management Working Group, Cumulative Environmental Management Association, Fort McMurray, Alberta.

Winter, T.C. 1989. Hydrologic studies of wetlands in the northern prairie. *In* Northern prairie wetlands. *Edited by* A. van der Valk. Iowa State University, Ames, Iowa. pp. 16–54.

Winter, T.C., Rosenberry, D.O., and LaBaugh, J.W. 2003. Where does the groundwater in small watersheds come from? Ground Water, **41**(7): 989–1000.

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The response of two remote, temperate lakes to changes in atmospheric mercury deposition, sulfate, and the water cycle

C.J. Watras and K.A. Morrison

Abstract: Atmospheric deposition is the ultimate source of Hg to many remote lakes, but the response to depositional change remains uncertain because of potential buffering by historical pools of Hg in sediments and soils. We investigated the responsiveness of two lakes over time scales ranging from weeks to decades. For waterborne Hg, results indicated that a precipitation-dominated seepage lake and a wetland-dominated drainage lake responded similarly to depositional change, despite high loadings of terrigeneous matter to the drainage lake. For methylmercury (meHg), the response was more complicated, reflecting the influence of multiple factors on in-lake methylation. In the seepage lake, waterborne meHg was correlated with the atmospheric deposition of $Hg^{(II)}$ and SO_4, and there was an indirect dependence on the water cycle. In the drainage lake, although wetland export was always the dominant external source of meHg, mass balance indicated that net in-lake methylation was four- to seven-fold greater than loading from the wetland. However, in-lake meHg production was related to the export of $Hg^{(II)}$, SO_4, dissolved organic carbon, and P from the wetland to the lake. The results suggest that atmospheric Hg deposition, weather, and microbial activity interactively effect the aquatic mercury cycle in ways that can be independent of historical pools of Hg in catchments.

Résumé : Les dépôts atmosphériques constituent la source ultime de Hg dans plusieurs lacs retirés, mais la réaction de ces lacs aux changements dans les dépôts atmosphériques reste incertaine à cause d'un tamponnage potentiel par les pools historiques de Hg dans les sédiments et les sols. Nous avons étudié la réactivité de deux lacs à diverses échelles temporelles allant de semaines à des décennies. Nos résultats de Hg en solution aqueuse indiquent qu'un lac alimenté par l'infiltration et dominé par les précipitations et un lac alimenté par le drainage et dominé par les terres humides réagissent de façon semblable aux changements dans les dépôts atmosphériques, malgré l'apport considérable de matière terrigène au lac de drainage. Dans le cas du méthyl-mercure (MeHg), la réaction est plus compliquée, ce qui reflète l'influence de facteurs multiples sur la méthylation au sein du lac. Dans le lac d'infiltration, la quantité de MeHg en solution aqueuse est reliée aux dépôts atmosphériques de $Hg^{(II)}$ et de SO_4 et elle dépend indirectement du cycle de l'eau. Dans le lac de drainage, même si l'apport provenant des terres humides est toujours la source externe dominante de MeHg, le bilan massique indique que la méthylation nette au sein du lac représente 4 à 6 fois l'apport des terres humides. Cependant, la production de MeHg dans le lac est reliée à l'exportation de $Hg^{(II)}$, de SO_4, de DOC et de P des terres humides vers le lac. Nos résultats laissent croire que les interactions des dépôts atmosphériques de Hg, des conditions climatiques et de l'activité microbienne affectent le cycle aquatique du mercure d'une façon qui peut être indépendante des pools historiques de Hg dans les bassins versants.

[Traduit par la Rédaction]

Introduction

It has long been acknowledged that the aquatic mercury cycle in remote and otherwise pristine lakes is dominated by atmospheric inputs, whether delivered directly to the water surface or delivered indirectly via terrestrial runoff (Baeyens et al. 1996; Fitzgerald et al. 1998). The re-emission of Hg across the air–water or air–soil interface accounts for significant loss from some ecosystems, but the major sinks for atmospherically deposited Hg are generally sediments and soils. As a result, there are large reservoirs of historically deposited Hg in many remote catchments, and their mobility remains uncertain (Hintelmann et al. 2002; Grigal 2003; Mason et al. 2005). Some models indicate that remobilization of excess Hg now stored in watershed soils and lake sediments could prevent the recovery of lakes for decades or even centuries (Meili et al. 2003). Other evidence suggests that Hg buried in soils and sediments is strongly sequestered and relatively immobile. This evidence includes (*i*) the conservative behavior of Hg in dated cores (Engstrom et al. 1994), (*ii*) the low concentration of Hg in groundwater (Krabbenhoft and Babiarz 1992), (*iii*) the short residence time

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of Hg in the water column of lakes (Watras et al. 1994), (*iv*) high particle–water distribution coefficients (Grigal 2002), and (*v*) the low mobility of Hg in soil-leaching experiments (Matilainen et al. 2001; Miretzky et al. 2005).

For precipitation-dominated seepage lakes, studies in northern Wisconsin support the hypothesis that mercury concentrations in water and fish can respond rapidly to depositional changes over time scales of less than a decade. For example, in Little Rock Lake (LRL), substantial declines in waterborne total Hg (Hg_T) and fish Hg were observed between 1994 and 2000, and these declines were largely attributable to contemporaneous changes in atmospheric Hg deposition (Watras et al. 2000; Hrabik and Watras 2002). These findings implied that the recycling of Hg from sediments was not the major source of waterborne Hg nor did it dominate the bioaccumulation process. In LRL, there was also evidence that seasonal changes in waterborne Hg_T followed the annual cycle of atmospheric Hg deposition, which suggested that Hg deposition might govern the aquatic Hg cycle on a time scale of months rather than years (Watras et al. 2002, 2006).

For drainage lakes, a large body of evidence dating back to seminal studies in Scandinavia and Canada indicates that runoff can be a large source of Hg_T (Mierle 1990; Verta 1990; Lindqvist 1991). Correlations between organic carbon (OC) of terrestrial origin and Hg_T in runoff and lake water have been reported in many studies, reflecting the strong affinity and cotransport of Hg_T and OC from terrestrial catchments in Europe and North America (Grigal 2002). These observations demonstrate the importance of terrigeneous organic matter as an Hg transport vector, and they suggest that the response to depositional change could be attenuated or overwhelmed by the export of historical Hg from catchment soils via runoff water if the relationship between Hg and OC remained constant over time. Furthermore, in watersheds disturbed by agriculture, forestry, or urbanization, the transport of particulate Hg via eroded soil particles can be substantial, and particulate Hg loads might contribute significantly to the waterborne Hg pool in drainage lakes unless they rapidly sink, taking their Hg burden with them into sediments (Kolka et al. 2001; Porvari et al. 2003; Balogh et al. 2005).

The purpose of this paper is to further constrain the response time of a well-studied, precipitation-dominated seepage lake (LRL) and to determine whether a drainage lake within the same airshed responds similarly to changes in atmospheric Hg deposition. The study lakes were selected to represent surface waters with low and high degrees of terrestrial influence. Mass balance was the principal tool in this investigation, and because water budgets largely dictate the exchange of solutes between lakes, airsheds, and watersheds, we focused on relationships between the water cycle and the aquatic mercury cycle, including the cycle of waterborne meHg — the chemical form that biomagnifies in aquatic food webs.

Materials and methods

Study sites

The two study lakes were Little Rock Lake (LRL) in Vilas County, Wisconsin (46°00′N, 89°37′W), and Devils Lake (DL) located 75 km southeast of LRL in Forest County (45°33′N, 88°50′W). Both lakes are situated in undeveloped, forested watersheds overlain by glacial tills that vary in thickness from 30 to 90 m (Attig 1985). The lakes support warm-water fisheries of bass (*Micropterus salmoides*) and perch (*Perca flavescens*).

Little Rock Lake is an 18 ha, clear-water, seepage lake with hydrologic inputs that are overwhelmingly dominated by direct deposition (~99%; Rose 1993). The biogeochemistry and ecology of LRL have been studied since 1984, when the lake was physically divided into two basins for experimental investigations (Brezonik et al. 1993; Frost et al. 2006; Sass et al. 2006). Surface water quality characteristics of both basins are now similar, and low solute concentrations reflect the influence of direct precipitation: Hg_T ~ 1 ng·L^{-1}, meHg ~ 0.1 ng·L^{-1}, pH ~ 6.0, ANC ~ 20 μequiv.·L^{-1}, dissolved organic carbon (DOC) ~ 3 mg·L^{-1}; SO_4 ~ 2.5 mg·L^{-1}, and conductivity ~ 12 μS·cm^{-1}. The average residence time of water in LRL is ~4 years (volume/input).

Devils Lake is a 12 ha, dystrophic, drainage lake with a water budget that is dominated by a seasonal tributary stream that flows from spring melt through summer and occasionally late fall. The tributary originates in a 24 ha headwater wetland located ~0.5 km upgradient from the lake. Hydrologic studies indicate that DL and its tributary stream are elevated above the local water table, so groundwater discharge is negligible and the flow path from the wetland to the lake is relatively direct (Horsley & Witten Inc. 2003). The surface waters of DL reflect a strong wetland influence: Hg_T ~ 3 ng·L^{-1}, meHg ~ 0.3 ng·L^{-1}, pH ~ 5.6, acid-neutralizing capacity (ANC) ~ 25 μequiv.·L^{-1}, DOC ~ 10 mg·L^{-1}; SO_4 ~ 2.8 mg·L^{-1}, and conductivity ~ 20 μS·cm^{-1}. The tributary stream is darker, more acidic, and enriched in mercury, consistent with a direct wetland source: Hg_T ~ 9 ng·L^{-1}, meHg ~ 0.3 ng·L^{-1}, pH ~ 4.1, ANC ~ −90 μequiv.·L^{-1}, DOC ~ 30 mg·L^{-1}; and SO_4 ~ 1.6 mg·L^{-1}. Water is discharged from DL via groundwater recharge and outflow through a single distributary stream. The average residence time of water in DL is ~1 year.

Field methods

Wet atmospheric Hg deposition was monitored weekly at three US NADP/NTN atmospheric monitoring sites (WI36, WI09, and WI32) following the standard MDN collection protocol (http://nadp/sws.uiuc.edu/mdn). LRL is located ~5 km southwest of WI36, and DL is centrally located 50–75 km southeast, southwest, and north of WI36, WI09, and WI32, respectively. Bulk Hg deposition was also monitored near LRL and DL using identical weekly sampling and analysis protocols (Morrison et al. 1995). For LRL, an IVL-type bulk Hg deposition collector (Jenson and Iverfeldt 1994) has been located at WI36 since 1994. For DL, an identical bulk collector was located ~2 km from the lake and operated from May 2002 through August 2004. Local weather was monitored at WI36 for LRL and at the Laona 6SW weather station about 13 km east of the lake (ID 474582, Wisconsin State Climatology Office, www.aos.wisc.edu/~sco/) for DL. Atmospheric meHg deposition was estimated from monthly integrated MDN collections at WI36 from 2002 through 2004.

Lake water was sampled by pumping at a central sampling station in each lake using a submersible, nonmetallic pump and following the Hg-clean protocol described previously (Watras et al. 2005, 2006). The water was prescreened through 64 μm, acid-cleaned Nitex netting to remove zooplankton. Water in the DL tributary stream was collected

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weekly by grab sampling beginning at the onset of spring melt and continuing until the stream stopped flowing in summer or fall. All water sampling for Hg conformed to method 1669 of the US Environmental Protection Agency (US EPA 1996).

Tributary and distributary stream discharge was calculated from continuous stage recordings (15-min intervals using baro-compensated, electronic data logging, water-level sensors) and stage–discharge (*S/D*) relationships that were established following the US Geological Survey (USGS) protocol for mini-Price "AA" flow meters with top-set wading rod. Discharge was manually measured weekly in the tributary and distributary stream to produce the *S/D* rating curves. Manual stage determinations were made periodically to validate the logger data. Continuous stage recordings were also made in the lake and related to lake volume using hypsometric curves (Horsley & Witten Inc. 2003).

Analytical methods

Lake-water, stream-water, and precipitation samples were analyzed for total Hg (Hg_T) and meHg using purge trap – CVAFS and ethylation – isothermal GC – CVAFS as in US EPA methods 1630 and 1631. Method detection limits (MDL) at the Trout Lake laboratory were 0.05 ng·L^{-1} (pooled variance of reagent blanks) for both Hg_T and meHg. On-going precision (mean ± standard deviation, SD) for Hg_T was 99.7% ± 6.2%, n = 735, and for meHg was 100.4% ± 10.5%, n = 609. Particulate and dissolved Hg_T and meHg were determined using dual filtration to collect particles directly on 0.4 µm Hg-clean filters (Morrison and Watras 1999), unless otherwise stated. The MDL for HgP was 22.3 ± 9.2 pg (n = 44), and duplicate relative percent differences (RPDs) averaged 27% ± 30% (n = 128); for meHgP, the MDL was 1.1 ± 2.4 pg (n = 49), and duplicate RPDs averaged 28.2% ± 0.05% (n = 92). Certified reference material (CRM) yields for HgP and meHgP (DOLT-2) were 100.6% ± 7% (n = 18) and 101.1% ± 0.2% (n = 14), respectively. All analyses for Hg_T and meHg conformed to the protocols and QA/QC requirements of US EPA methods 1630 and 1631 (US EPA 2001, 2002).

Ancillary solutes and water quality variables were determined following methods described previously (Watras et al. 2005, 2006). Briefly, pH was measured in a closed cell using a glass combination electrode designed for low ionic strength waters. Suspended particulate matter (SPM) was determined on oven-dried (60 °C), preweighed 0.4 µm membrane filters using a Cahn C-31 microbalance. DOC was determined on samples filtered through precombusted 0.4 µm glass fiber filters. The filtered samples were wet-oxidized with sodium persulfite and heated to 200 °C, and the liberated CO_2 was measured with an NDIR detector. Anions (SO_4, NO_3, Cl) were determined by ion chromatography (US EPA method 300.0). Cations (Ca, Mg, Mn, Fe, Al, Na) were measured by ICP (SM 3120B). Potassium was measured with SM 3111B. Total Kjeldahl N (TN) and total P (TP) were measured using US EPA methods 351.2 and 365.1, respectively.

Budgets

Water budgets for both lakes were based on the following mass balance expression:

$$(1) \qquad \Delta S = (P + G_i + \mathrm{RO} + Q_i) - (E + G_o + Q_o)$$

where ΔS is change in storage over time (usually 1 year), P is precipitation, G_i is groundwater discharge, RO is runoff, Q_i is streamflow in, E is evaporation, G_o is groundwater recharge, and Q_o is streamflow out. The detailed water budgets for LRL compiled by Rose (1993) for a 7-year period that included both wet and dry years were adopted by applying contemporaneous precipitation data. Water budgets for DL were based on the methods of Horsley & Whitten Inc. (2003). Briefly, precipitation amount was monitored at the Laona 6SW weather station. Lake storage volume was calculated as a function of lake stage and lake bathymetry. Tributary and distributary flow were monitored continuously as described above. Nonchannelized runoff was estimated for the 12.3 ha nearshore portion of the DL watershed by applying a runoff coefficient of 0.1 that was derived from the annual water yield for the full tributary subcatchment.

Mercury budgets (Hg_T) were based on a similar expression:

$$(2) \qquad \Delta S = (P + G_i + \mathrm{RO} + Q_i) - (E' + S_e + G_o + Q_o)$$

where ΔS and the input and output terms now refer to waterborne mercury mass (E' is gaseous Hg evasion, and S_e is Hg sedimentation). Inputs via atmospheric deposition and streamflow (P and Q_i) were estimated as the product of volume-weighted concentrations of Hg in precipitation or stream water and the volume of precipitation or stream water discharge over a given time interval. Based on the respective water budgets, G_i was considered negligible for both lakes. RO in DL was calculated as the nonchannelized runoff volume times the volume-weighted concentration of mercury in the tributary stream. G_o was the product of groundwater outflow volume and the mean concentration of mercury in the epilimnion (assuming only littoral recharge). E' and S_e were estimated as a pooled residual loss term ($E' + S_e$) after the other terms were computed. The waterborne mass of mercury in each lake was determined as the sum of masses over all depths sampled on a given date, according to $\Sigma c_i v_i$, for $i = 1$ to n, where c and v represent the concentration and volume, respectively, for a given depth stratum after adjusting for changes in lake stage.

Budgets for waterborne meHg included a term for net methylation in the lake (M_{net}) but no evasion term, such that

$$(3) \qquad \Delta S = (P + G_i + \mathrm{RO} + Q_i) - (S_e + G_o + Q_o) + M_{net}$$

For meHg, S_e was estimated as 1% of the residual loss term from the Hg_T budget, as meHg constitutes roughly 1% of the Hg_T in sediments (Ullrich et al. 2001). Because demethylation in sediments is not considered, S_e is probably a lower limit for sedimentation loss from the water column. Given estimates or measurements for the other terms, M_{net} was calculated as

$$(4) \qquad M_{net} = \Delta S + (S_e + G_o + Q_o) - (P + G_i + \mathrm{RO} + Q_i)$$

Thus, M_{net} is a conservative estimate of the mass of meHg in the water column attributable to in-lake production, regardless of whether the site of production is in the water or in sediments. By definition, M_{net} includes demethylation in the water column.

Data analysis

Time series for Hg_T, meHg, and other solutes in multiyear data sets were investigated graphically by plotting individual

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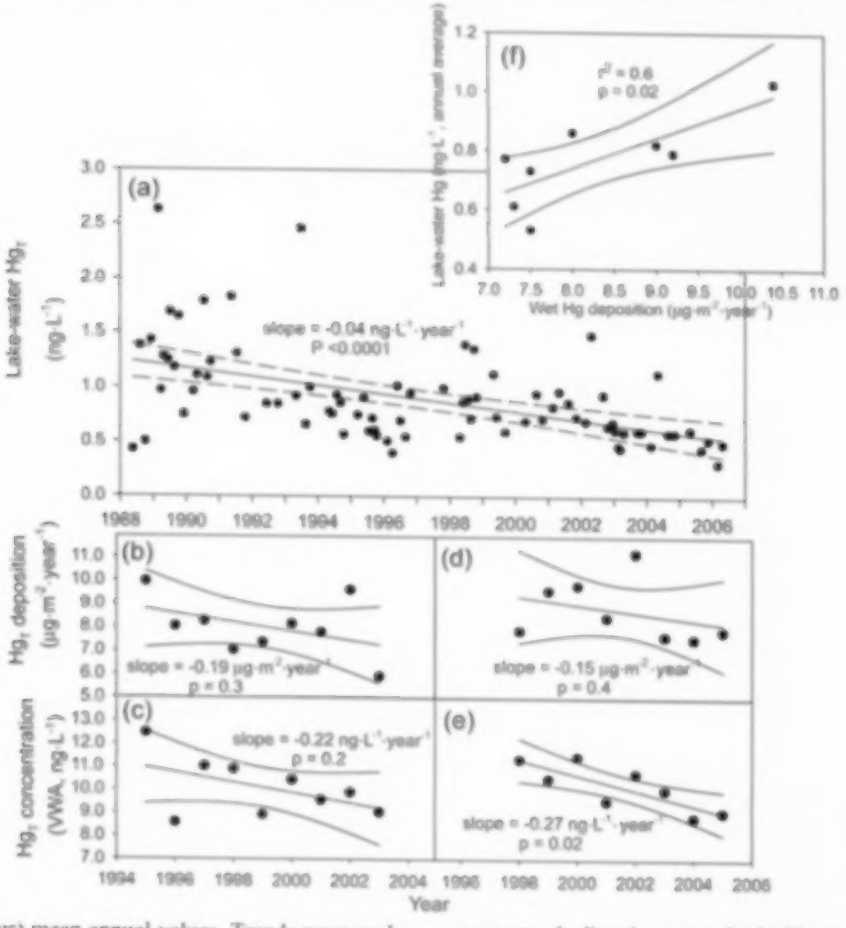
Fig. 1. Long-term time trends for waterborne Hg_T in Little Rock Lake, 1988–2006, and atmospheric Hg deposition at WI36: (*a*) waterborne Hg_T in the unstratified LRL south basin; (*b*) IVL bulk atmospheric Hg deposition; (*c*) concentration of Hg_T in IVL bulk deposition; (*d*) MDN wet-only atmospheric Hg deposition; (*e*) concentration of Hg_T in MDN wet-only deposition; (*f*) correlation between waterborne Hg_T in LRL south and wet Hg deposition at WI36, 1997–2005. VWA, volume-weighted average for year.



observations and (or) mean annual values. Trends were evaluated using linear regression, and the Durban–Watson statistic was used to detect autocorrelation in the residuals. When a breakpoint was visually apparent in a time plot, the time series was segmented and linear models were fit separately to each segment. The probability of non-zero slope (p) at $\alpha = 0.05$ was reported for all time series regressions, along with the value of the slope and (or) coefficient of determination (r^2). All graphical and statistical analyses were performed using SigmaPlot 9.0 and SigmaStat 3.1 (SPSS Inc., Chicago, Illinois).

Results and discussion

Little Rock Lake (LRL)

In precipitation-dominated LRL, there has been a gradual downward trend in waterborne Hg_T since at least 1988 ($p < 0.0001$, Durban–Watson statistic = 1.9; Fig. 1*a*). The rate of decline for the 19-year period was –0.04 ng·L^{-1}·year^{-1}, unchanged from that reported 6 years ago for the period ending in 1999 (Watras et al. 2000). In the earlier report, a contemporaneous decline in atmospheric Hg deposition also was noted, and this depositional decline has continued to 2006 (Figs. 1*b*–1*e*). However, the time series for atmospheric Hg deposition is still relatively short (~10 years) and variability is high due largely to year-to-year changes in precipitation amount. Although declining trends are evident in Figs. 1*b*–1*e*, they are not statistically significant, except perhaps for the volume-weighted concentration of Hg_T in wet deposition (VWC), which has declined by about 0.3 ng·L^{-1}·year^{-1} since 1996 ($p = 0.02$, Durban–Watson statistic = 3.3; Fig. 1*e*). A decline in VWC implies a progressive change in pollutant strength within the local airshed or in the reactions that govern net Hg_T deposition, independent of precipitation amount. The cause of such changes remains unclear.

Despite the high year-to-year variability in depositional rates, there was a significant positive relationship between lake-water Hg_T and wet Hg_T deposition over a decadal time scale ($p = 0.02$; Fig. 1*f*). Because other environmental factors can have strong effects on the concentration of Hg_T in lake water, especially factors governing Hg loss by evasion and sedimentation, such factors could potentially confound a

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Fig. 2. Annual cycle of waterborne Hg_T in LRL (●) and annual cycle of wet Hg deposition (shaded bars), 1994–2004: (*a*) stratified north basin; (*b*) unstratified south basin. Precipitation data are the seasonal running averages (13 weeks).

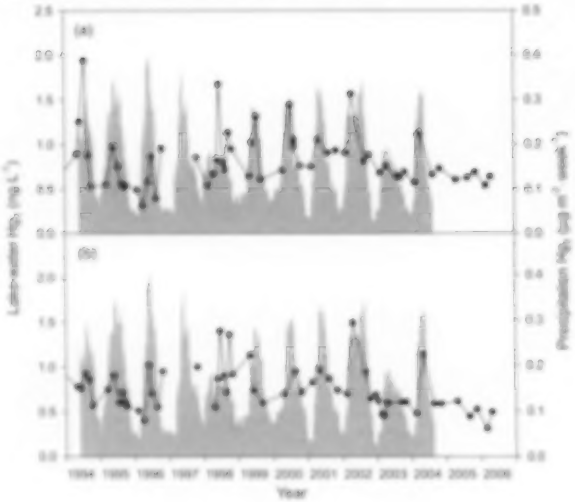
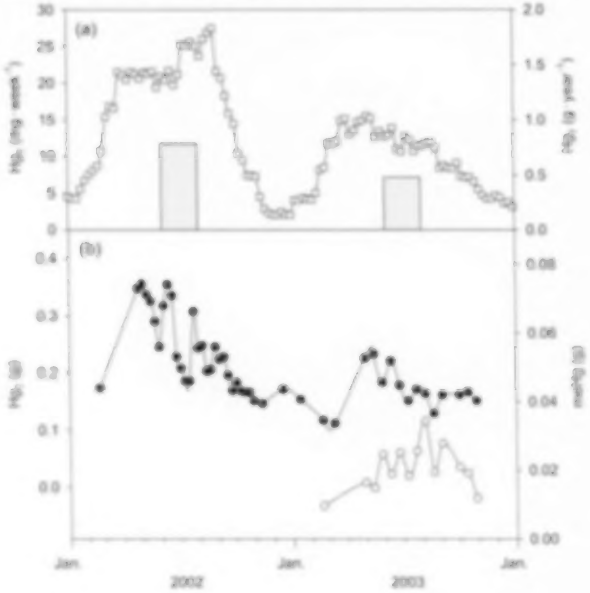


Fig. 3. Weekly changes in (*a*) atmospheric Hg_T deposition (□) and (*b*) waterborne Hg_T (●) and meHg (○) in LRL, 2002–2004. Shaded bars in (*a*) are annual atmospheric Hg_T deposition. Lake data in (*b*) are whole-lake masses for the unstratified south basin.



causal relationship between waterborne Hg_T and atmospheric deposition. However, as shown below, ancillary data for LRL indicate that these other loss-related factors cannot easily explain the observed trend in waterborne Hg_T, implying that it has been governed principally by atmospheric Hg deposition.

Observations for LRL also indicate that atmospheric Hg deposition and waterborne Hg_T in LRL were temporally coherent over time scales of less than 1 year (Fig. 2). Lake data collected seasonally for the past 13 years confirm earlier observations made from 1995 to 2000 (Watras et al. 2002). The observed annual cycle of waterborne Hg_T in LRL results from a dynamic balance between external inputs and internal loss processes. If there was no loss during summer and fall, waterborne Hg_T would rise until ice-on and then level off when the lake was sealed from further atmospheric input. Based on the water budget of Rose (1993), we estimate that waterborne Hg_T would increase toward a steady-state concentration of about 30 ng·L^{-1} over a period of several years, if it behaved as a conservative solute. Instead, the observed annual cycle implies that loss processes, such as evasion and sedimentation, remove Hg_T much faster than it is resupplied from the atmosphere during summer. Low but stable concentrations of waterborne Hg_T during winter suggest that removal rates decrease under ice, increasing the average residence time of waterborne Hg_T. Although seasonal sampling is sufficient to demonstrate synchrony between the aquatic Hg_T cycle and the atmospheric Hg deposition cycle, the amplitudes of the two cycles are not directly comparable because significant changes in the lake may occur over shorter time scales.

To investigate coherence between atmospheric Hg deposition and lake-water Hg_T over very short time scales, the well-mixed basin of LRL was sampled weekly during open water from 2002–2004 (Fig. 3). During this time, annual atmospheric Hg deposition to LRL declined by 38%, and waterborne Hg_T in the lake declined by a similar amount (–27%). The lower atmospheric Hg deposition observed in 2003 resulted from lower amounts of precipitation (–33%) and from lower concentrations of Hg in rain (–10%). Fine structure in the time series for waterborne Hg_T suggests that changes in the balance between input and loss processes affected waterborne Hg_T over very short time scales (i.e., days to weeks). For example, the large increase in waterborne Hg_T that began during ice-out in both years was associated with a sharp rise in depositional loading (Fig. 3). Direct atmospheric deposition contributed roughly 200 and 150 mg Hg to the lake during early spring in 2002 and 2003, respectively, and waterborne Hg_T increased by 180 and 120 mg over the same time intervals. Snow and ice covering the lake likely contributed additional Hg_T during spring melt. Although that contribution was not quantified rigorously, a rough estimate can be obtained by multiplying the volume of snow on the lake (as liquid water, 5–10 cm deep) by 4 ng Hg·L^{-1} (from earlier snow sampling; Bloom and Watras 1989). This approximation yields a snowpack contribution of about 15–30 mg Hg (five- to 10-fold less than the contemporaneous depositional load). After spring melt, weekly atmospheric Hg deposition was sufficient to account for most of the other fine-scale features in the LRL time series. Two notable exceptions are the large upswings observed in early June and mid-July during 2002. Upswings of 72 and 122 mg in waterborne Hg_T occurred in LRL during these two 1-week periods, respectively. Contemporaneous atmospheric deposition could account for only 21% of the June upswing and 66% of the July upswing. These two exceptions remain unresolved.

The potentially confounding influence of other environmental factors on the gradual 19-year decline in waterborne

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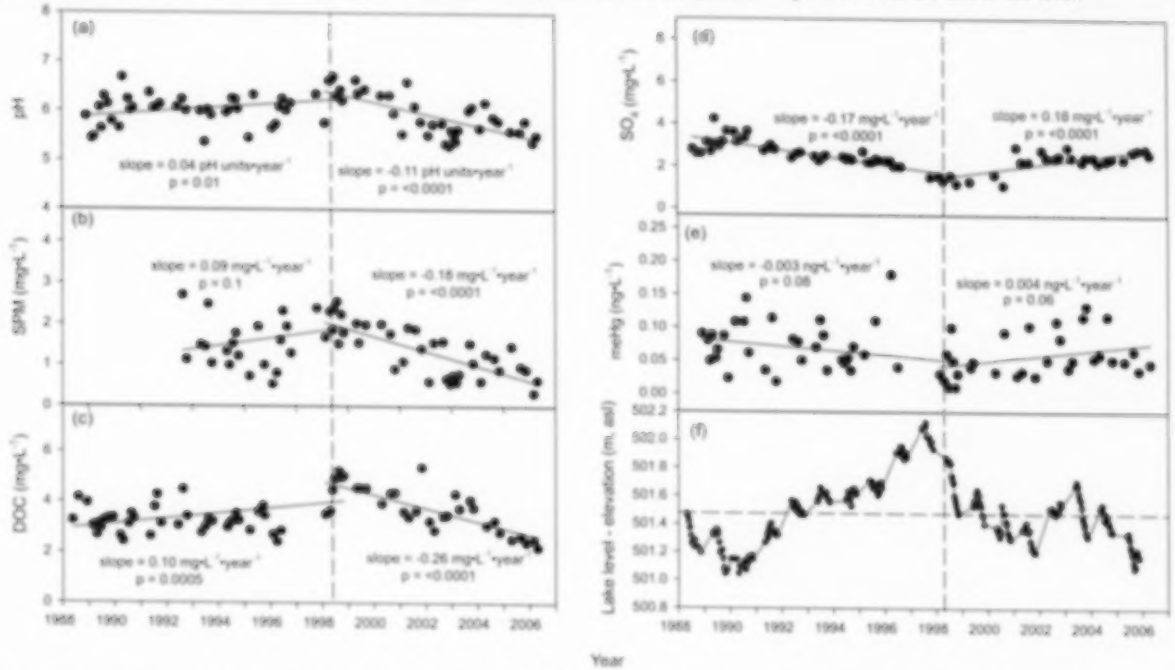
Fig. 4. Biphasic time trends for water quality variables in LRL (unstratified south basin) in relation to the local water cycle, 1988–2006. Broken vertical line indicates onset of declining lake levels, 1998–2006. Lake-level changes (*f*) shown for nearby reference lake where stage measurements are made biweekly. Broken horizontal line indicates time-weighted average lake level. asl, above sea level.



Hg_T was investigated by examining time trends for pH, SPM, and DOC. Previous studies indicate that an increase in pH or SPM could result in greater loss by evasion or sedimentation (Fitzgerald et al. 1991; Hurley et al. 1991; Vandal et al. 1991), and a decrease in DOC could result in less organic complexation and lower storage (Hudson et al. 1994). However, linear regression analysis of LRL data over the 19-year time period indicated significant declines in pH (–0.02 units·year^{-1}, $p = 0.05$) and SPM (–0.07 mg·L^{-1}·year^{-1}, $p = 0.001$) and a modest increase in DOC (0.02 mg·L^{-1}·year^{-1}, $p = 0.3$). Because these trends run in the opposite direction of that expected to cause an increase in rates of Hg_T loss, they cannot easily explain the 19-year decline in waterborne Hg_T.

Closer inspection of the data for pH, SPM, and DOC in LRL indicates that the time trends for these variables were biphasic, rather than monotonic (Figs. 4*a*–4*c*). The major breakpoints in these three time series all occur in 1998, coinciding with a transition in the regional water cycle from high-water to drought conditions (Fig. 4*f*). Before 1997 when lake levels were rising, pH was gradually increasing, whereas SPM and DOC were relatively stable, but as the lake level receded during drought, pH, SPM, and DOC all declined. Previous studies in this region have attributed analogous changes in lake-water chemistry to diminished groundwater discharge and (or) increased evapoconcentration during drought (e.g., Kenoyer and Anderson 1989; Wentz et al. 1995; Webster et al. 1996). For LRL, the observed decrease in DOC likely resulted from reduced contact with riparian vegetation as the lake level receded, and the observed decrease in SPM (which is mostly living and detrital plankton) coincided with a decline in total P concentration ($p < 0.01$). The drought-related decrease in pH is less easily explained.

Because groundwater discharge is a negligible component of the LRL water budget even when the regional water table is high (≤1%; Rose 1993), decreased groundwater input of base cations seems an unlikely cause of declining pH during drought. Indeed, from 1998–2006, there were slight, albeit statistically insignificant, increases in the concentration of Ca, Mg, and Mn and no detectible changes in two of the major anions (Cl, NO_3). However, the concentration of SO_4 in LRL increased by 0.18 mg·L^{-1}·year^{-1} during drought (Fig. 4*d*), despite significant declines in the atmospheric deposition of SO_4 and H^+ (–0.26 kg^{-1} SO_4·ha^{-1}·year^{-1} and –0.0004 kg H^+·ha^{-1}·year^{-1}; $p < 0.01$), the dominant external source of SO_4 and H^+ (Brezonik et al. 1993). Evapo-concentration can explain some but not all of the increase in SO_4 concentrations during the low-water years. Because the volume of LRL is about 30% greater at maximum stage (Rose 1993), evaporative concentration could result in a 30% increase in solute concentrations, all other things being equal. However, during the recent drought, there was a 93% increase in waterborne SO_4 concentration (1.5 to 2.9 mg·L^{-1}) and an unexplained 48% increase in the waterborne SO_4 mass (383 to 566 kg SO_4).

A similar change in SO_4 was reported by Urban et al. (2001) for LRL during an earlier drought (1986–1991). As the lake entered drought in mid-1986, there was an upswing in lake-water SO_4 concentrations from 2.7 to 3.4 mg·L^{-1} (roughly 0.17 mg·L^{-1}·year^{-1} over 4 years). Annual mass balances constructed by Urban et al. (2001) indicate that variable out-seepage of SO_4 could explain some of the drought

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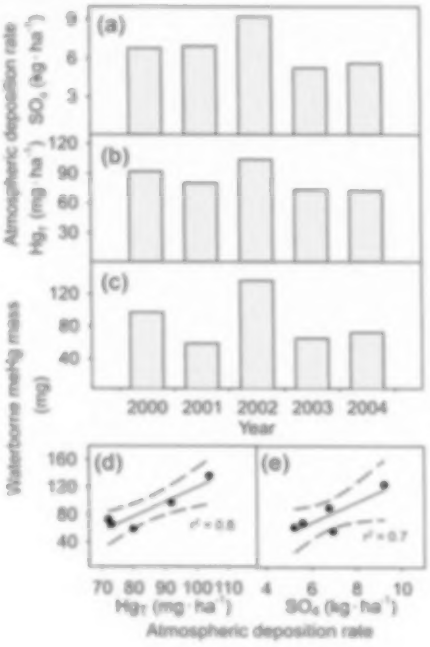
effect, but the factor explaining most of the upswing in S storage during low-water years was net sediment burial. Although year-to-year variability in the estimate of burial was large, the mass balances suggest that it declined by approximately fourfold during drought. It is unclear whether a diminished sink or a drought-induced source of SO_4 to the lake mediated this decline. For some catchments, drought has been shown to cause the reoxidation of reduced S stored in exposed sediments and riparian wetland, which can be flushed into surface waters during episodes of high precipitation or snowmelt, thereby driving pH down (Devito et al. 1999). For LRL, the reoxidation and export of about 0.5 g $S \cdot m^{-2} \cdot year^{-1}$ would be needed to account for the observed increase in SO_4 concentration. Assuming a sulfur inventory of 1–2 mg $S \cdot g^{-1}$ in exposed littoral sediment (cf. Baker et al. 1992; Urban and Monte 2001; Urban et al. 2001), mobilizing ~1% to ~2% of the S in the top 4 cm would be required each year.

Although the mechanism governing SO_4 concentrations during drought remains unknown, we hypothesize that increased concentrations in the water column would stimulate an increase in rates of SO_4 reduction (SRR), creating some degree of negative feedback. SSRs have been shown to be linearly related to waterborne SO_4 at the concentrations observed in LRL (Baker et al. 1988; Kelly et al. 1997; Urban and Monte 2001). In the shallow well-mixed basin, SO_4 reduction would be expected to occur primarily in the surficial layer of profundal sediments, where the oxic–anoxic transition occurs near the sediment–water interface (Brezonik et al. 1993; Sherman et al. 1994; Urban et al. 2001). Because this zone also appears to be the major site for $Hg^{(II)}$ methylation in shallow lakes, meHg production would be expected to increase with the increase in SRR (Gilmour et al. 1992). Thus, we further hypothesize that the observed increases in waterborne meHg and SO_4 were causally linked during low-water years (Figs. 4*d*, 4*e*). It is unlikely that the increase in meHg was a direct result of drought per se, as neither groundwater dynamics nor evapo-concentration can account for the observed 75% increase in waterborne meHg from 1997–2006 (0.04 to 0.07 $ng \cdot L^{-1}$).

Further evidence of a direct relationship between meHg and SO_4 in LRL is also shown (Fig. 5). Between 2002 and 2004, there was a short-term increase in precipitation that caused a transient rise in water levels (Fig. 4*f*) and an increase in the atmospheric deposition of Hg and SO_4 to LRL (Figs. 5*a*, 5*b*). The waterborne mass of meHg in the stratified north basin (where meHg is produced at high rates within the anoxic hypolimnion) increased as well (Fig. 5*c*), so that over the 5-year period from 2000 to 2004, waterborne meHg was positively correlated with the atmospheric loading of $Hg^{(II)}$ and SO_4 (Figs. 5*d*, 5*e*). This finding strongly suggests a connection between meHg production, Hg deposition, and SO_4 deposition over relatively short time scales under natural field conditions, which is consistent with the findings of experimental SO_4 enrichment studies in LRL (Watras et al. 2006).

We conclude that changes in atmospheric Hg deposition had substantial effects on the aquatic mercury cycle in this precipitation-dominated seepage lake over relatively short periods of time. Impacts on the aquatic cycle of meHg were complicated by factors that co-mediate the methylation of atmospherically derived $Hg^{(II)}$. A hitherto underappreciated factor is the water cycle, especially its indirect role in regulating the availability of substrates for meHg production during high-water and low-water years. Thus, transient, drought-related variability can confound relationships between long-term trends in atmospheric Hg deposition, net meHg production, and potentially, bioaccumulation.

Fig. 5. Relationship between waterborne meHg and the atmospheric deposition of Hg_T and SO_4 to the stratified north basin of LRL, 2000–2004.



Devils Lake (DL)

For this wetland-dominated drainage lake, investigations focused on four questions. (*i*) How did the lake respond to annual changes in atmospheric Hg deposition? (*ii*) Was the aquatic mercury cycle similar to that observed in the seepage lake or was it fundamentally different? (*iii*) Was there evidence of terrestrial mercury being "mined" from the watershed and delivered to the lake via runoff? (*iv*) Was the headwater wetland the dominant source of meHg to the lake, masking the effect of depositional change in the lake itself? To address these questions, we first examined budgets for water, Hg_T, and meHg compiled for three consecutive years when atmospheric Hg deposition and runoff varied by ~30% and ~50%, respectively.

Annual budgets in DL

In all three years, streamflow in and streamflow out were the dominant terms in the water budget of DL (Table 1*a*). Tributary flow was also the major source of Hg_T to the lake, supplying on average about 60% of the annual Hg input (range 46% to 68%; Table 1*b*). Topographically defined, the terrestrial catchment for the tributary stream is relatively large (~260 ha), and given the rate of wet atmospheric Hg

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Table 1. Budgets for water, mercury, and methylmercury in Devils Lake.

(*a*) Annual hydrologic budgets for Devils Lake, 2002–2004.

	Inputs			Outputs			
Year	Precipitation (P)	Streamflow (Q_i)	Surface runoff (RO)	Streamflow (Q_o)	Lake seepage[a] (GO)	Evaporation (E)[b]	Change in lake storage (ΔS)
2002	124.0	287.3	16.9	319.0	38.5	66.0	4.8
2003	90.4	128.9	7.6	175.7	10.5	66.0	−25.3
2004	108.2	129.0	7.6	163.4	17.2	66.0	−1.8
Mean	107.6	181.7	10.7	219.4	22.1	66.0	−7.4
SD	16.8	91.4	5.4	86.5	14.6	6.2	15.8

(*b*) Annual budgets for waterborne total mercury (Hg_T) in Devils Lake, 2002–2004.

	Inputs			Outputs			
Year	Precipitation (P)	Streamflow (Q_i)	Surface runoff (RO)	Streamflow (Q_o)	Lake seepage (GO)	Net sedimentation and evasion (Se + Ev)[b]	Change in storage (ΔS)
2002	1.50	3.27	0.19	0.91	0.11	3.62	0.33
2003	1.01	0.91	0.05	0.62	0.04	1.85	−0.52
2004	0.99	1.18	0.07	0.53	0.06	1.47	0.18
Mean	1.17	1.79	0.11	0.69	0.07	2.31	0.00
SD	0.29	1.29	1.29	0.20	0.04	1.15	0.46

(*c*) Seasonal budgets for waterborne meHg in Devils Lake, 2002–2004.

	Inputs			Outputs			
Year	Precipitation (P)	Streamflow (Q_i)	Net methylation (M)	Streamflow (Q_o)	Lake seepage (GO)	Net sedimentation (Se)[b]	Change in storage (ΔS)
2002[c]	12	56	405	66	4	27	378
2003[d]	7	27	150	78	2	9	96
2004[e]	7	23	104	48	2	11	73
Mean	9	35	219	64	3	16	183
SD	3	18	162	15	1	10	170

Note: Units: (*a*) 10^3 m^3; (*b*), grams; (*c*), milligrams.
[a]Residual term.
[b]Based on mean and SD for LRL from Rose (1993).
[c]10 April – 19 August.
[d]26 March – 18 August.
[e]29 March – 17 August (nonchannelized surface runoff ignored: <3% Q_i).

deposition (~10 μg·m^{-2}·year^{-1}), it is clear that the forest was a net sink for Hg_T. Most of the Hg_T in precipitation (~95%) was sequestered either in soils or vegetation, evaded back into the atmosphere, or transported to deep groundwater. Because throughfall and litterfall typically deliver more Hg_T to the forest floor than direct precipitation during any given year (presumably because of sorption processes in the canopy, as reviewed by Grigal 2002), the terrestrial watershed was likely an even stronger sink for Hg_T than the precipitation data imply.

The total amount of water and Hg_T delivered to DL declined substantially between 2002 and 2003, reflecting the combined effect of changes in precipitation and runoff (Tables 1*a*, 1*b*). Inputs of Hg_T to DL via direct precipitation declined by ~30% (as observed for LRL), but the major change was in fluvial Hg loading, which declined by ~70%, yielding a total load reduction of ~60%. Despite the large change in external loading, the time-averaged waterborne pool of Hg_T in the lake declined by a modest 13% (Table 2).

The modest change in pool and large change in load imply that the average residence time of Hg in the water column increased with decreasing inputs (roughly twofold, from 0.2 to 0.4 years; Table 2). Because streamflow was dominant during the high-loading year, this observation suggests that fluvial inputs were lost more rapidly from the water column than direct pluvial inputs. Comparison with LRL tends to support this hypothesis. In LRL, changes in Hg loading were driven almost entirely by changes in direct precipitation, and when annual inputs declined by ~30%, the residence time of waterborne Hg remained relatively constant at 0.3 ± 0.02 years (range; Table 2).

If there was no fluvial input to DL, the Hg residence time would likely increase further due to the high DOC content of DL water (ca. 10 mg DOC·L^{-1} vs. 2.5 mg·L^{-1} in LRL). As a strong ligand, terrigeneous DOC is known to compete effectively with binding sites on settling particulate matter, the primary vector transporting Hg to sediments in Wisconsin lakes (Hurley et al. 1991; Hudson et al. 1994). For comparison, the residence time for Hg in a nearby dark-water seepage lake was estimated to be ~0.8 years (Russett Lake, DOC = 6.8 mg·L^{-1}; Watras et al. 1994). Longer residence times per se could buffer the response of dark-water lakes to depositional change by lengthening the period of the aquatic Hg cycle.

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Table 2. Annual input–output balance (*I/O*) and residence time for waterborne Hg_T in Devils Lake (DL) and Little Rock Lake (LRL, south basin).

Lake	Year	In-lake Hg_T pool[a] (g)	Total inputs (g)	Total outputs (g)	*I/O*	Residence time[b] (years)
DL	2002	1.08	4.96	4.63	1.1	0.22
	2003	0.94	1.97	2.51	0.8	0.47
	2004	0.93	2.24	2.06	1.1	0.43
LRL	2002	0.22	0.78	0.81	~1	0.28
	2003	0.16	0.48	0.48	~1	0.33

[a]Time-weighted annual average.
[b]Pool/inputs.

Seasonality in DL

The seasonal pattern of atmospheric Hg deposition was similar at the three MDN sites in north-central Wisconsin, and there was reasonable agreement with the on-site IVL bulk collectors, indicating a regionally coherent depositional regime dominated by precipitation inputs (Fig. 6*a*). For 75 weeks of co-deployment, Hg_T concentrations in bulk and wet deposition were 13.3 ± 1.4 and 13.1 ± 1.2 ng·L^{-1}, respectively (mean ± standard error, SE), and the volume-weighted average Hg concentrations were 10.7 and 11.2 ng·L^{-1}, respectively (±0.9 SD among the three MDN sites).

The seasonal loading of Hg_T to DL closely followed the tributary hydrograph (Figs. 6*b*, 6*c*), as observed in many northern catchments (as reviewed by Grigal 2002). The fluvial flux of all measured solutes increased linearly with hydrologic discharge, largely because discharge rates varied by much more than solute concentrations (Fig. 7; Table 3). As a result of very high discharge rates during spring melt, most of the fluvial Hg_T flux occurred in spring, when 60% to 75% of the annual tributary load was delivered to the lake. During spring, tributary inputs exceeded Hg_T storage in the water column by a factor of 1.4 to 3.5, depending on the amount of snowmelt and early precipitation. When fluvial loading was highest in 2002, only 25% of the spring load remained in the water column and the rest was lost mainly by sedimentation and evasion. In contrast, when fluvial loading was lowest in 2003, roughly 50% of the spring load remained waterborne and the other 50% was lost mainly by outflow. These observations suggest that a large fraction of the fluvial Hg_T rapidly settled out or evaded back into the atmosphere. As a result, the buildup of waterborne Hg_T during the spring was attenuated relative to external loading, in contrast to LRL, where most of the spring load remained in the water column until summer.

Although fluvial inputs were the dominant source of Hg_T to DL, seasonal changes in waterborne Hg_T closely followed the cycle of atmospheric Hg deposition, as observed in LRL (Fig. 6*d*). This may reflect, in part, the frequency of lake sampling, but it suggests that similar environmental factors and internal processes drove the annual cycles of waterborne HgT in both lakes. The annual cycles of waterborne meHg were also similar in both lakes. Waterborne meHg rose to peak concentrations in late summer, lagging behind waterborne Hg_T by several weeks (Figs. 3*b* and 6*d*). This time lag reflected the development of stratified microbial communities in the anoxic hypolimnia of both lakes. Preliminary studies using DNA analysis to determine pelagic microbial community composition have suggested that similar microbiological assemblages were associated with meHg in these hypolimnia and that the assemblages comprised deltaproteobacteria (Kent et al. 2006). Thus, the timing of peaks in waterborne meHg was likely related to the strongly seasonal activity of methylating microbes in deep anoxic waters (Eckley et al. 2005; Watras et al. 2005; Eckley and Hintelmann 2006).

The tentative answer to our first two questions, then, is that the aquatic mercury cycle was similar in DL and LRL, and it responded to changes in atmospheric Hg deposition over similarly short time scales. However, the degree of response may reflect fundamental differences in hydrology. In the drainage lake, most of the inflowing water quickly flowed out during early spring via the distributary stream, carrying some waterborne Hg_T with it. A large fraction of the remaining Hg_T quickly settled out or evaded, so that only 25% to 50% of the spring pulse remained in the water column. In contrast, most of the Hg_T that entered LRL during spring remained in the water column until summer, elevating the time-weighted waterborne mass in a manner more directly proportional to depositional loading. It is not yet clear why fluvial Hg_T inputs were lost so quickly during spring in DL, but high losses during spring melt suggest that the settling of particulate Hg_T into alluvial fans may be an important factor.

Transport processes in the DL catchment

In tributary stream water, the concentration of Hg_T varied significantly between years from 11.7 ± 3.3 in 2002, to 7.2 ± 0.9 in 2003, and 8.7 ± 1.2 ng·L^{-1} in 2004 (mean ± SD; analysis of variance, ANOVA, $F = 16.24$, df = 2,40, $p < 0.01$; Table 4). However, the concentration of Hg_T was relatively constant within a given year, and it did not covary with either DOC or hydrologic discharge (Figs. 8*a*, 9), similar to reports for some wetland-dominated streams in Minnesota and Ontario (Kolka et al. 2001; Galloway and Branfireun 2004). Hg_T concentrations in the DL tributary were similar to those in concurrent precipitation (Table 4). Over the full study period, only two values in stream water exceeded 12 ng·L^{-1} (<5% of all observations). Both of these high values occurred in the high-flow year of 2002 (Fig. 8), and on both dates, particulate Hg comprised ~50% of the Hg_T (Table 4). Otherwise, most of the Hg_T in stream water was functionally dissolved (<0.4 µm; Table 4). SPM determinations indicated low particulate loads, ranging from about 0.5 to 2.5 mg·L^{-1} (Table 5).

The concentration of Hg_T in DL tributary water was at the high end of the range reported for forest streams in Sweden and for larger rivers in Wisconsin where positive correlations

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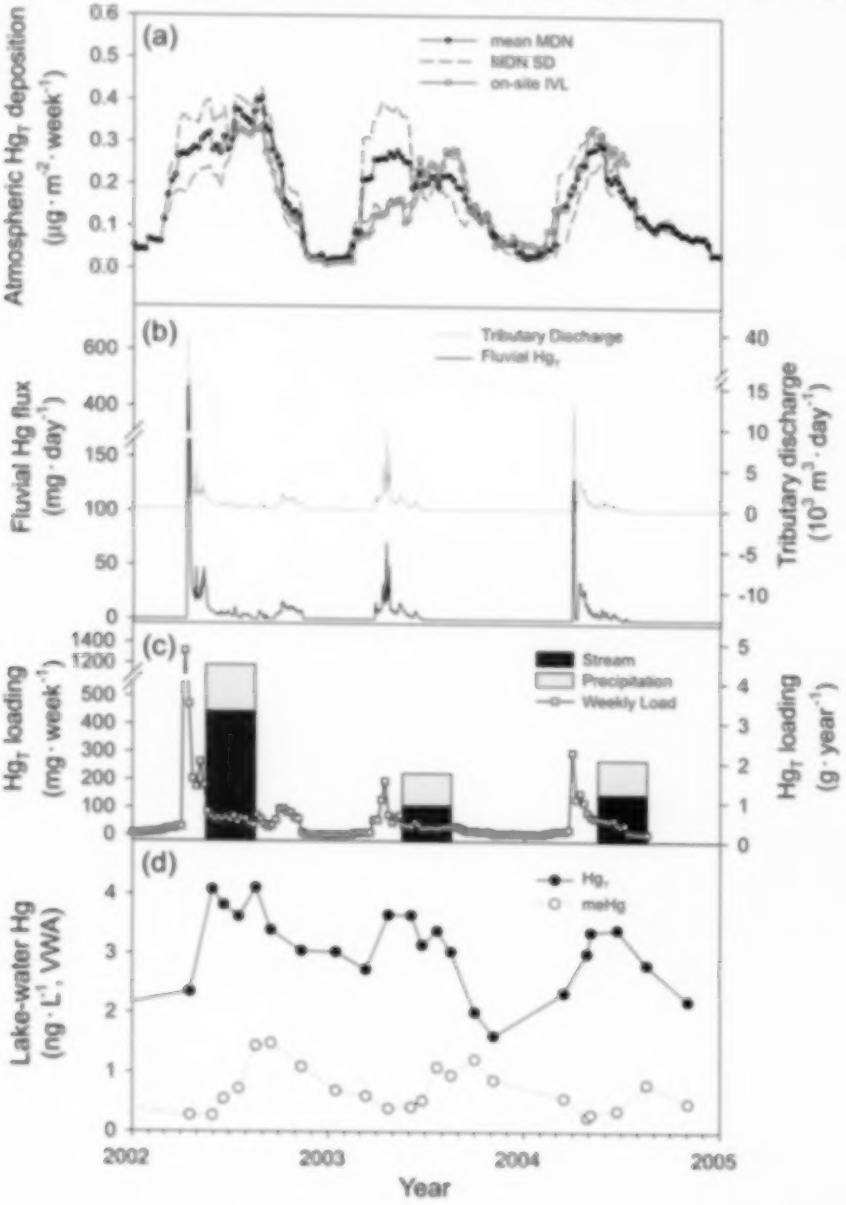
Fig. 6. Three-year time series for mercury at Devils Lake (DL), 2002–2004. (*a*) Atmospheric Hg deposition (solid circles and broken lines indicate running weekly mean and SD for wet deposition at MDN sites WI36, WI12, and WI10; open circles indicate bulk Hg_T deposition on-site). (*b*) Fluvial Hg_T flux (solid line, daily Hg_T flux; shaded line, daily water discharge). (*c*) Total Hg_T loading to DL, weekly and annual, via pluvial and fluvial sources. (*d*) Annual cycles of waterborne Hg_T and meHg in DL. VWA, volume-weighted average.



with DOC have been observed (Meili 1991; Babiarz et al. 1998). The lack of correlation between waterborne Hg_T and DOC in the DL tributary (and in some other woodland streams with high concentration of terrigeneous DOC, ~25 to >60 mg·L^{-1}; see Grigal 2002) raises the question of how these observations can be reconciled with numerous reports of a strong positive correlation in lake and stream waters. Given that TOM is the dominant source of DOC and a strong sink for Hg_T, slow vertical flow paths from the forest floor though mineral soils should strip both solutes from solution and yield low concentrations in discharge waters. On the other hand, faster lateral flow paths across wetted organic soils should yield relatively high concentrations of both solutes. If precipitation largely sets an upper limit for waterborne Hg_T, a positive correlation between Hg_T and DOC would be expected to break down as fluvial Hg_T ap-

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Fig. 7. Relationship between hydrologic discharge rate and solute transport via the DL tributary stream, 2003. Broken horizontal lines indicate the average concentration of Hg_T and meHg in rain during this time period.

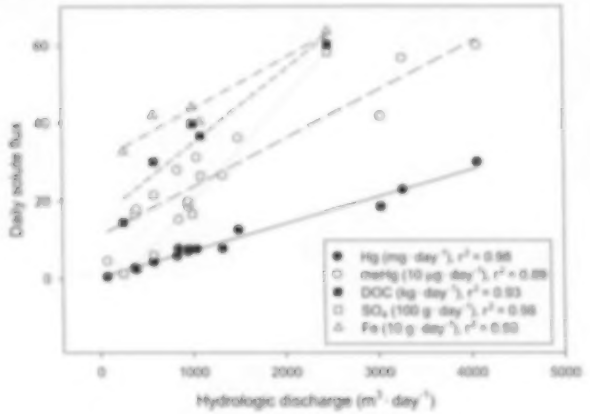
Daily solute flux
Hydrologic discharge (m³ · day⁻¹)
Hg (mg · day⁻¹), r² = 0.98
meHg (10 µg · day⁻¹), r² = 0.89
DOC (kg · day⁻¹), r² = 0.93
SO4 (100 g · day⁻¹), r² = 0.98
Fe (10 g · day⁻¹), r² = 0.50

Table 3. Correlation of fluvial solutes with hydrologic discharge rate or with date (proxy for temperature or biological activity) in the DL tributary stream.

	Correlate (r)[a]			
	Hydrologic discharge		Day number	
Solute	Concentration	Flux	Concentration	Flux
Al	–0.83	0.96	0.99	–0.97
Ca	–0.88	0.99	0.99	–0.92
Mn	–0.61	0.99	0.89	–0.87
Mg	–0.89	0.99	0.99	–0.91
Na	–0.86	0.99	0.98	–0.90
Total N	–0.93	0.99	0.95	–0.94
SO_4	0.76	0.99	–0.97	–0.86
K	0.95	0.98	–0.88	–0.85
Cl	ns	0.98	ns	–0.79

Note: ns, not significant.
[a]Sign denotes slope.

proaches the concentration in precipitation, as observed in the DL tributary and the S2 watershed in Minnesota (Kolka et al. 2001). Because high binding constants for aqueous Hg–DOC complexes indicate that almost all of the waterborne Hg would be associated with either colloidal or truly dissolved OC and cotransported from the DL headwater wetland (e.g., Haitzer et al. 2003; Skyllberg et al. 2003), a progressive decrease in the ratio of Hg to DOC from spring through summer suggests that the two solutes were regulated by different processes (Fig. 9).

The release of DOC from terrestrial plant tissues and soil solids represents a balance between in situ production, adsorption, desorption, and microbial utilization, with in situ production resulting from physical leaching and microbial exoenzymes (Moore and Dalva 2001). Laboratory data for DOC release rates from various forest floor – wetland substrates (Moore and Dalva 2001) suggest that shallow flow paths across relatively fresh organic material during summer would be expected to yield high concentrations of DOC in wetland export water, as we observed, whereas dilution by high flows across degraded debris during snowmelt could explain the low DOC concentrations that we observed in spring. In contrast, the relatively constant concentrations of waterborne Hg_T in wetland export water may reflect the shallow hydrologic flow path of relatively recent rain or melt waters, their short contact time with soil solids, and the large excess of strong organic ligands in solution.

A recent pluvial source of fluvial Hg_T would be consistent with the elevated hydrologic position of DL and its tributary, which both lie above groundwater level (Horsley & Witten Inc. 2003). The stream does not gain water as it flows to the lake. Instead, roughly 25% of the stream-water volume is lost to groundwater, whereas solute concentrations remain constant over the 0.5 km distance (Horsley & Witten Inc. 2003). Monitoring wells suggest that groundwater flows under the lake and tributary toward the outlet stream, as reported for several other lakes situated in the deep tills (30–60 m) of northern Wisconsin (Magnuson et al. 2006). The DL headwater wetland is fed by direct rainfall, runoff, and interflow from surrounding upland soils, and it discharges water directly into the sloping tributary streambed at a single point. Although the hydrologic flow path through the wetland is uncertain, horizontal flow is likely greatest near the surface given the low hydrologic conductivity of deeper, compacted wetland soils (Freeze and Cherry 1979).

The finding of low particulate Hg_T in DL stream water is contrary to observations for some watersheds, but even in watersheds where soil erosion is high, the broader significance of particulate Hg transport is unclear. Although it is widely acknowledged that the ultimate source of Hg associated with soil matter is atmospheric (Grigal 2002), eroded particles transport an unknown mix of "old" and newly deposited Hg. Some insight into this mix may be gained from particle–water partition coefficients for Hg_T in the DL tributary. An apparent particle–water distribution coefficient can be calculated as

$$(5) \qquad K_d(\mathrm{L \cdot kg^{-1}}) = \frac{[\mathrm{Hg_P}](\mathrm{ng \cdot L^{-1}})}{[\mathrm{SPM}](\mathrm{kg \cdot L^{-1}}) \cdot [\mathrm{Hg_D}](\mathrm{ng \cdot L^{-1}})}$$

where the subscripts P and D refer to particulate and dissolved Hg fractions, respectively. Based on eq. 5, the net exchange of Hg between terrigeneous particles and rain water (Δ[Hg], ng·L^{-1}) can be estimated for a given K_d according to

$$(6) \qquad \Delta[\mathrm{Hg}] = \frac{[\mathrm{SPM}] \cdot (K_d \cdot [\mathrm{Hg_D}] - [\mathrm{HgP}])}{K_d \cdot [\mathrm{SPM}] + 1}$$

by setting Hg_D to the concentration in precipitation and then assigning reasonable values for SPM and the Hg burden of particulates (HgP, ng·kg^{-1}). Thus, eq. 6 can be used to investigate the conditions under which terrigeneous particles would release or sequester Hg_T during stream transport, provided the kinetics of equilibration are sufficiently fast.

Because of the strong affinity of Hg for particulate organic matter (POM), K_d is remarkably consistent across a wide variety of surface waters (log K_d = 5.1 ± 0.4, mean ± SD; Grigal 2002). Likewise, HgP in forest floor and mineral soil horizons across northern Minnesota and Wisconsin varies over fairly narrow ranges, from about 100 to 250 ng·g^{-1}

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Table 4. Comparison of mercury in precipitation and DL tributary stream water.

		Precipitation		Stream water			
Year	Chemical form	Concentration ($ng \cdot L^{-1}$)	Deposition ($\mu g \cdot m^{-2}$)	Mean ($ng \cdot L^{-1}$)	SD	n	% Dissolved mean (range)
2002	Hg_T	12.1±0.9	9.7±1.1	11.7	3.3	16	76 (45–99)
	meHg	0.06	0.05	0.45	0.19	16	81 (57–100)
2003	Hg_T	11.2±1.9	7.1±1.3	7.2	0.9	14	89 (86–95
	meHg	0.20	0.13	0.27	0.13	13	90 (85–97)
2004	Hg_T	9.1±0.4	6.6±0.6	8.7	1.2	13	93 (84–100)
	meHg	0.11	0.08	0.23	0.09	10	92 (70–100)

Note: Precipitation Hg_T is the mean ± standard deviation (SD) for MDN sites WI36, WI09, and WI32 (concentration volume-weighted). Precipitation meHg is for WI36 only. Stream water was sampled weekly for n weeks starting at onset of spring melt. Dissolved < 0.4 μm.

Fig. 8. Concentrations of waterborne (*a*) Hg_T and (*b*) meHg in the DL tributary, 2002–2004.

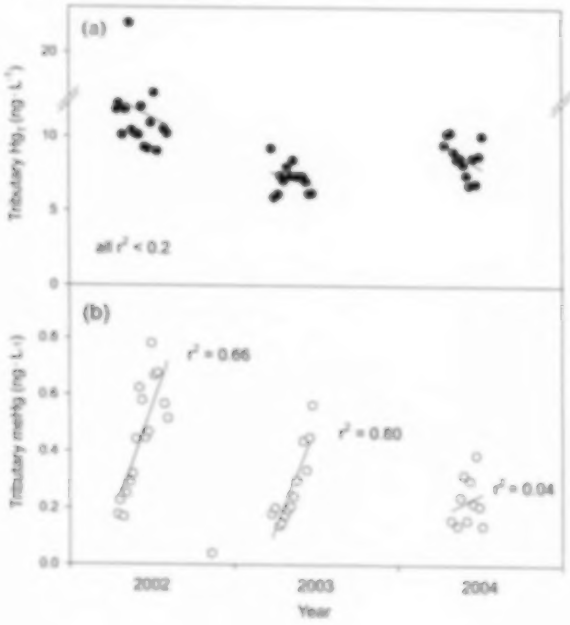
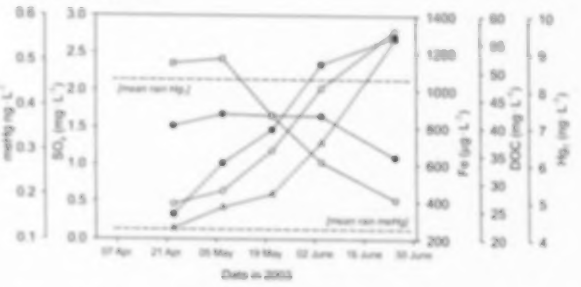


Fig. 9. Time series for waterborne mercury and other solutes in DL tributary stream water, 2003 (meHg, ○; SO_4, □; Fe, △; DOC, ■; Hg_T, ●).



and 15 to 30 $ng \cdot g^{-1}$, respectively (Nater and Grigal 1992). Hg concentrations in living vegetation (tree leaves and stems) tend to be intermediate between forest floor and mineral soil material (Grigal 2002). Assuming reasonable values for Hg in particulate matter and for K_d in stream water, eq. 6 predicts that particulate Hg burdens could rise to >600 $ng \cdot g^{-1}$ when eroded particles were mixed into a stream of ambient rain water (~8–10 $ng \cdot L^{-1}$), provided that the mass of SPM was low (Fig. 10). If the mass of SPM became extraordinarily high (i.e., muddy water), the Hg burden of suspended particulates would increase only slightly. Nonetheless, because the particles would acquire Hg when washed into the stream, rather than releasing it into the water, this exercise implies that "old" Hg sequestered by forest soils is an unlikely source of dissolved Hg in the DL tributary. Field data confirm that suspended particles in the tributary stream had substantially higher Hg burdens than expected for native soils (~350–600 $ng \cdot g^{-1}$; Table 5).

Re-equilibration of fluvial particulates with the more dilute lake water would be expected as they entered the lake and began to settle. Given Hg_D concentrations in the lake of 2.9 ± 0.04 $ng \cdot L^{-1}$ (Table 5), eq. 6 predicts a transfer of Hg back into the lake water. However, it also predicts that the particles would not lose more Hg than they had gained while in the stream. Direct observations are consistent with these predictions. Particles in the lake had consistently lower Hg burdens than particles in the stream measured simultaneously, and the Hg burden of particles in the lake was within the range expected for native soil particles (Table 5). A prevalence of autochthonous particulates in the lake (living and dead plankton) complicates the above scenario, but does not necessarily discount it. Campbell et al. (1997) showed that terrigeneous DOC tends to coagulate on plankton cells in dark water lakes, and this phenomenon could explain the similarity in K_d between lake and stream water. SPM in both waters would have functionally similar surface coatings despite different origins.

meHg in the DL catchment

The cycle of waterborne meHg differed from the cycle of Hg_T in both lake water and tributary stream water. Although waterborne Hg_T remained relatively constant in the tributary from spring though summer, the concentration of meHg increased with time after spring melt (Fig. 8*b*), as observed for meHg in wetland outflows in Canada, the northeastern US, and Sweden (e.g., Driscoll et al. 1998; Lee et al. 2000;

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Table 5. Particle–water partitioning of mercury in the DL tributary stream and DL lake water during 2003.

Date	SPM (mg·L^{-1})	Hg_P (ng·L^{-1})	Hg_D (ng·L^{-1})	HgP (ng·g dw^{-1})	Log K_d Hg_T	$meHg_P$ (ng·L^{-1})	$meHg_D$ (ng·L^{-1})	meHgP (ng·g dw^{-1})	Log K_d meHg	DOC[a] (mg·L^{-1})	SO_4 (mg·L^{-1})
Stream											
23 April	2.5±0.1	1.0±0.02	6.0	410	4.83	< 0.02[b]	0.17	<8[b]	4.30	24	2.4
07 May	0.9±0.1	0.5±0.02	6.8	610	4.95	0.02	0.19	25	5.12	33	2.4
21 May	0.7±0.1	0.3±0.02	6.9	550	4.90	0.05	0.25	68	5.43	40	1.7
04 June	1.1±0.3	0.4±0.01	6.9	340	4.70	0.02±0.01	0.42	13	4.50	51	1.0
25 June	1.7±0.6	0.7±0.12	5.5	390	4.85	0.04±0.01	0.33	23	4.63	56	0.5
Mean ± SD	1.3±0.7	0.6±0.3	6.5±0.6	460±110	4.85±0.10	0.03±0.02	0.31±0.16	32±24	4.80±0.47	41±13	1.6±0.8
Lake											
23 April	3.5±0.1	0.9±0.01	2.8	250	4.94	0.12±0.01	0.28	34	5.08	11	2.8
07 May	3.8±0.1	0.8±0.06	2.9	220	4.88	0.19±0.00	0.29	48	5.23	12	2.8
21 May	2.5±0.0	0.5±0.03	3.2	210	4.82	0.16±0.00	0.23	62	5.43	12	2.7
04 June	1.5±0.1	0.4±0.04	3.1	240	4.88	0.08±0.01	0.28	51	5.29	13	2.7
25 June	3.6±0.0	0.5±0.09	2.2	140	4.80	0.09±0.01	0.29	26	4.95	13	2.7
Mean ± SD	3.0±1.0	0.6±0.2	2.9±0.4	210±50	4.86±0.06	0.13±0.04	0.27±0.02	44±14	5.19±0.18	12±1	2.8±0.0

Note: Data for each date are mean values ± range of duplicates. Hg_D and $meHg_D$ (dissolved fraction) estimated by difference from duplicate determinations of total and particulate fractions on each date. Grand means are not volume-weighted. Stream pH = 4.1 on all dates; lake pH = 5.4 to 5.6. Lake data for surface waters only. Data was rounded after computations were performed.

[a]Below detection limit, not included in mean ± SD calculation.

Fig. 10. Hypothetical exchange of Hg_T between fluvial particulates and water in the DL tributary stream based on eq. 6. Mercury-laden particles (HgP) are assumed to originate from the forest floor, and stream water originates from recent precipitation or snowmelt. Solid diagonal line indicates the equilibrium condition in the stream when log K_d = 5. Hatched box indicates a range of initial conditions typical for the Great Lakes region. Solid arrows indicate trajectories from one set of initial conditions (solid circle) toward equilibrium given low or high SPM. Open circles indicate actual field data for five dates with broken arrows tracking back to starting conditions based on eq. 6. Trajectories of broken arrows imply that terrestrial particles acquired substantial amounts of mercury when washed into the stream. Open rectangles and dotted arrows indicate hypothetical fate of the average Hg-laden stream particle upon entering DL lake water. Hg acquired in the stream is desorbed upon entering the more dilute lake water, but the particle does not lose its original Hg burden. Empirical observations of particulate Hg_T are consistent with the hypothetical result. Hg_D, dissolved Hg.

Branfireun and Roulet 2002). The meHg concentration in DL tributary water increased to concentrations three- to five-fold higher than those in precipitation, indicating a terrestrial source, whereas fluvial Hg_T concentrations were typically below those in rain (Fig. 9; Table 4). MeHg constituted 1.5% ± 1.3% of the Hg_T in precipitation (mean ± SD of 36 monthly composite samples from 2002–2004), with an average monthly concentration of 0.15 ± 0.25 ng·L^{-1} and an average monthly deposition rate of 7.6 ± 12.2 ng·m^{-2}.

As the concentration of meHg and most other fluvial solutes increased from spring to summer, the concentration of SO_4 in stream water decreased (Fig. 9), presumably because of increased SO_4 reduction in wetland pore waters. Negative correlations between meHg and SO_4 have been reported in other studies of wetland streams (Branfireun and Roulet 2002; Galloway and Branfireun 2004), and experimental additions of SO_4 to wetlands have been shown to increase the yield of meHg (Branfireun et al. 1999; Harmon et al. 2004;

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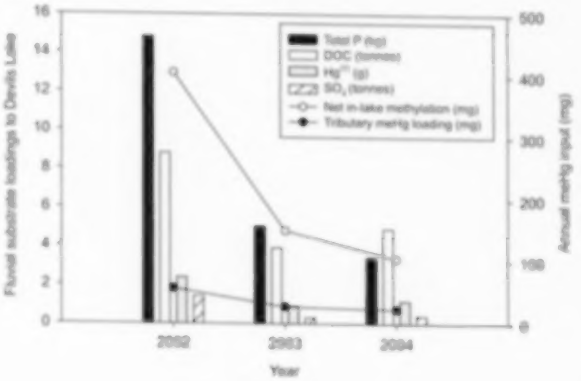
Jeremiason et al. 2006). High concentrations of SO_4 in spring runoff reflect the predominant atmospheric source and perhaps an "ionic pulse" during snowmelt (Dommergue et al. 2003). Other solutes originating primarily from terrestrial sources (Al, Ca, Mn, Mg, and Na) were apparently diluted in spring melt waters.

As the annual atmospheric Hg deposition and runoff amount declined between 2002 and 2004, meHg in wetland export waters also declined (Fig. 8), as did the accumulation of waterborne meHg in the lake (Fig. 6). The mean concentration of meHg in tributary water and the fluvial flux of meHg to DL both dropped by substantially more than the decline in atmospheric Hg deposition over this time period (~50%; Tables 1*c*, 4). Lee et al. (2000) made similar observations in the Svartberget catchment in northern Sweden, noting that hydrologic and biogeochemical processes may have a larger effect on the catchment output of meHg than changes in atmospheric Hg deposition. Data from the Svartberget and from boreal wetlands in Canada clearly show that meHg export increases when water flow traverses the upper horizon of organic-rich soils where meHg is presumably produced by microbial activity (Branfireun et al. 1996; Bishop and Lee 1997; Galloway and Branfireun 2004). However, variability in the load of atmospherically derived $Hg^{(II)}$ substrate cannot be discounted as a contributing factor.

Although runoff emanating from the large DL wetland was the major external source of water and meHg to DL every year, it was a relatively minor meHg source when compared to in-lake production. Mass balances showed that in-lake methylation accounted for ~80% of the meHg that accumulated in the water column each summer (Table 1*c*). The annual wetland export rate for meHg averaged 0.14 ± 0.07 $\mu g \cdot m^{-2} \cdot year^{-1}$ (normalized to wetland area) or 0.3 ± 0.15 $\mu g \cdot m^{-2} \cdot year^{-1}$ (normalized to lake area), rates consistent with those reported for other temperate–boreal watersheds influenced by wetlands (St. Louis et al. 1996; Driscoll et al. 1998; Lee et al. 1998). In contrast, in-lake meHg production rates (net) were fivefold higher than the estimated wetland export rate, on average 1.5 $\mu g \cdot m^{-2} \cdot year^{-1}$ (lake-area basis). Although the fluvial influx and in-lake production of meHg declined by similar amounts between 2002 and 2004 (–52% and –62%, respectively), the diminished pool of waterborne meHg in the lake was caused mainly by the change in in-lake methylation (Table 1*c*). Nevertheless, year-to-year variation in tributary flow may have indirectly mediated the amount of waterborne meHg produced in DL. As net in-lake methylation declined from 2002 to 2004, the fluvial loading of key microbial substrates declined as well ($Hg^{(II)}$, SO_4, DOC, and P), suggesting a synergistic biochemical effect similar to that observed in LRL (Fig. 11; Watras et al. 2006).

For meHg associated with SPM, there were notable differences between the DL tributary and the lake (Table 5). The meHg burden of lake particulates was roughly twofold higher than that of stream particles, and the partitioning of meHg to lake particles was significantly higher than partitioning in the stream (*t* test, $p < 0.01$). For lake particulates, meHg also partitioned more strongly than Hg_T, a result not observed in the stream, where both Hg species partitioned to SPM similarly. These observations suggest the preferential uptake and retention of meHg by living plankton in the lake that is consistent with other field and laboratory studies of bioaccumulation (Miles et al. 2001; Moye et al. 2003; Pickhardt and Fisher 2007).

Fig. 11. Annual inputs of meHg to DL via in-lake production and tributary loading, shown in relation to the annual fluvial loading of substrates necessary for microbially mediated $Hg^{(II)}$ methylation.



We conclude that atmospheric Hg deposition, precipitation patterns, and microbial activity can interactively have large effects on the aquatic mercury cycle in ways that are independent of the large historical pools of Hg in lake sediments and watershed soils. In this study, a precipitation-dominated seepage lake and a wetland-dominated drainage lake responded to depositional change over similar time frames, even though runoff containing large amounts of terrigeneous matter was the dominant external source of water, Hg_T, and meHg to the drainage lake. It remains to be seen whether seepage and drainage lakes in other hydrogeomorphic settings will behave similarly. For lakes with shorter water residence times, fed by wetlands with higher water yields, the balance between internal and external meHg inputs may shift to favor terrestrial sources. However, if the microbial processes governing $Hg^{(II)}$ methylation prove to be the same in anoxic hypolimnia, surficial sediments, and wetland porewaters, one might expect similar responses to changes in the atmospheric deposition of $Hg^{(II)}$, SO_4, and water.

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References

Attig, J.W. 1985. Pleistocene geology of Vilas County, Wisconsin. Wisconsin Geologic and Natural History Survey, Information Circular No. 50.

Babiarz, C.L., Hurley, J.P., Benoit, J.M., Shafer, M.M., Andren, A.W., and Webb, D.A. 1998. Seasonal influences on partitioning and transport of total and methylmercury in rivers from contrasting watersheds. Biogeochemistry, **41**: 237–257.

Baeyens, W., Ebinghaus, R., and Vasiliev, O. (*Editors*). 1996. Global and regional mercury cycles: sources, fluxes and mass balances. NATO ASI Series 2. Environment. Kluwer Academic Publishers, Dordrecht, Netherlands.

Baker, L.A., Pollman, C.D., and Eilers, J.M. 1988. Internal alkalinity generation and geochemical controls of Florida softwater lake chemistry. Water Resour. Res. **24**: 1069–1082.

Baker, L.A., Engstrom, D.R., and Brezonik, P.L. 1992. Recent sulfur enrichment in the sediments of Little Rock Lake, Wisconsin. Limnol. Oceanogr. **37**: 689–702.

Balogh, S.J., Nollet, Y.H., and Offerman, H.J. 2005. A comparison of total mercury and methylmercury export from various Minnesota watersheds. Sci. Total Environ. **340**: 261–270.

Bishop, K.H., and Lee, Y.-H. 1997. Catchments as a source of mercury/methylmercury in boreal surface waters. *In* Mercury and its effects on environment and biology. *Edited by* A. Sigel and H. Sigel. Marall Dekker, New York. pp. 113–130.

Bloom, N.S., and Watras, C.J. 1989. Observations of methylmercury in precipitation. Sci. Total Environ. **87/88**: 199–207.

Branfireun, B.A., and Roulet, N.T. 2002. Controls on the fate and transport of methylmercury in a boreal headwater catchment, northwestern Ontario, Canada. Hydrol. Earth Syst. Sci. **6**(4): 785–794.

Branfireun, B.A., Heyes, A., and Roulet, N.T. 1996. Hydrology and methylmercury dynamics of a Precambrian headwater peatland. Water Resour. Res. **32**(6): 1785–1794.

Branfireun, B.A., Roulet, N.T., Kelly, C.A., and Rudd, J.W.M. 1999. In situ sulphate stimulation of mercury methylation in a boreal peatland: toward a link between acid rain and methylmercury contamination in remote environments. Global Biogeochem. Cycles, **13**(3): 743–750.

Brezonik, P.L., Eaton, J.G., Frost, T.M., Garrison, P.J., Kratz, T.K., Mach, C.E., McCormick, J.H., Perry, J.A., Rose, W.A., Sampson, C.J., Shelley, B.C.L., Swenson, W.A., and Webster, K.E. 1993. Experimental acidification of Little Rock Lake, Wisconsin: chemical and biological changes over the pH range 6.1 to 4.7. Can. J. Fish. Aquat. Sci. **50**: 1101–1121.

Campbell, P.G.C., Twiss, M.R., and Wilkinson, K.J. 1997. Accumulation of natural organic matter on the surfaces of living cells: implications for the interaction of toxic solutes with aquatic biota. Can. J. Fish. Aquat. Sci. **54**: 2543–2554.

Devito, K.J., Hill, A.R., and Dillon, P.J. 1999. Episodic sulfate export from wetlands in acidified headwater catchments: prediction at the landscape scale. Biogeochemistry, **44**: 187–203.

Dommergue, A., Ferrari, C., Poissant, L., Gauchard, P.-A., and Boutron, C.F. 2003. Diurnal cycles of gaseous mercury within the snowpack at Kuujjuarapik/Whapmagoostui, Québec, Canada. Environ. Sci. Technol. **37**: 3289–3297.

Driscoll, C.T., Holsapple, J., Schofield, C.L., and Munson, R. 1998. The chemistry and transport of mercury in a small wetland in the Adirondack region of New York, USA. Biogeochemistry, **40**: 137–146.

Eckley, C.S., and Hintelmann, H. 2006. Determination of mercury methylation potentials in the water column of lakes across Canada. Sci. Total Environ. **368**: 111–125.

Eckley, C.S., Watras, C.J., Hintelmann, H., Morrison, K., Kent, A., and Regnell, O. 2005. Mercury methylation in the hypolimnetic waters of lakes with and without connection to wetlands in northern Wisconsin. Can. J. Fish. Aquat. Sci. **62**: 400–411.

Engstrom, D.R., Swain, E.B., Henning, T.A., Brigham, M.E., and Brezonik, P.L. 1994. Atmospheric mercury deposition to lakes and watersheds: a quantitative reconstruction from multiple sediment cores. *In* Environmental chemistry of lakes and reservoirs. Advances in Chemistry Series 237. *Edited by* L.A. Baker. American Chemical Society, Washington, D.C. pp. 33–66.

Fitzgerald, W.F., Mason, R.P., and Vandal, G.M. 1991. Atmospheric cycling and air–water exchange of mercury over mid-continental lacustrine regions. Water Air Soil Pollut. **56**: 745–768.

Fitzgerald, W.F., Engstrom, D.R., Mason, R.P., and Nater, E.A. 1998. The case for atmospheric mercury contamination in remote areas. Environ. Sci. Technol. **32**(1): 1–7.

Freeze, R.A., and Cherry, J.A. 1979. Groundwater. Prentice-Hall, Inc., Englewood Cliffs, N.J.

Frost, T.M., Fischer, J.M., Brezonik, P.L., Gonzalez, M.J., Kratz, T.K., Watras, C.J., and Webster, K.E. 2006. The experimental acidification of Little Rock Lake. *In* Long-term dynamics of lakes in the landscape. *Edited by* J.J. Magnuson, T.K. Kratz, and B.J. Benson. Oxford University Press, New York. pp. 168–186.

Galloway, M.E., and Branfireun, B.A. 2004. Mercury dynamics of a temperate forested wetland. Sci. Total Environ. **325**: 239–254.

Gilmour, C.C., Henry, E.A., and Mitchell, R. 1992. Sulfate stimulation of mercury methylation in freshwater sediment. Environ. Sci. Technol. **26**: 2281–2287.

Grigal, D.F. 2002. Inputs and outputs of mercury from terrestrial watersheds: a review. Environ. Rev. **10**: 1–39.

Grigal, D.F. 2003. Mercury sequestration in forests and peatlands: a review. J. Environ. Qual. **32**: 393–405.

Haitzer, M., Aiken, G.R., and Ryan, J.N. 2003. Binding of mercury (II) to aquatic humic substances: influence of pH and source humic substances. Environ. Sci. Technol. **37**(11): 2436–2441.

Harmon, S.M., King, J.K., Gladden, J.B., Chandler, G.T., and Newman, L.A. 2004. Methylmercury formation in a wetland mesocosm amended with sulfate. Environ. Sci. Technol. **38**(2): 650–656.

Hintelmann, H., Harris, R., Heyes, A., Hurley, J.P., Kelly, C.A., Krabbenhoft, D.P., Lindberg, S.E., Rudd, J.W.M., Scott, K.J., and St. Louis, V.L. 2002. Reactivity and mobility of new and old mercury deposition in a boreal forest ecosystem during the first year of the METAALICUS study. Environ. Sci. Technol. **36**(23): 503495040.

Horsley & Witten Inc. 2003. Devils Lake summary report: water years 1996 to 2002. Horsley & Witten Inc., 90 Route 6A, Sandwich, MA 02563, USA.

Hrabik, T.R., and Watras, C.J. 2002. Recent declines in mercury concentration in a freshwater fishery: isolating the effects of de-acidification and decreased atmospheric mercury deposition in Little Rock Lake. Sci. Total Environ. **297**: 229–237.

Hudson, R.J.M., Gherini, S.A., Watras, C.J., and Porcella, D.B. 1994. Modeling the biogeochemical cycling of mercury in lakes: the Mercury Cycling Model (MCM) and its application to the MTL study lakes. *In* Mercury pollution: integration and synthesis. *Edited by* C.J. Watras and J.W. Huckabee. Lewis Publishers, Chelsea, Michigan. pp. 473–526.

Hurley, J.P., Watras, C.J., and Bloom, N.S. 1991. Mercury cycling in a northern Wisconsin seepage lake: the role of particulate matter in vertical transport. Water Air Soil Pollut. **56**: 543–552.

Jenson, A., and Iverfeldt, Å. 1994. Atmospheric bulk deposition of mercury to the southern Baltic Sea. *In* Mercury pollution: inte-

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gration and synthesis. *Edited by* C.J. Watras and J.W. Huckabee. Lewis Publishers, Chelsea, Michigan. pp. 221–229.

Jeremiason, J.D., Engstrom, D.R., Swain, E.B., Nater, E.A., Johnson, B.M., Almendinger, J.E., Monson, B.A., and Kolka, R.K. 2006. Sulfate addition increases methylmercury production in an experimental wetland. Environ. Sci. Technol. **40**(12): 3800–3806.

Kelly, C.A., Rudd, J.W.M., Bodaly, R.A., Roulet, N.P., St. Louis, V.L., Heyes, A., Moore, T.R., Schiff, S., Aravena, R., Scott, K.J., Dyck, B., Harris, R., Warner, B., and Edwards, G. 1997. Increases in fluxes of greenhouse gases and methyl mercury following flooding of an experimental reservoir. Environ. Sci. Technol. **31**: 1334–1344.

Kenoyer, G.J., and Anderson, M.P. 1989. Groundwater's dynamic role in regulating acidity and chemistry in a precipitation-dominated lake. J. Hydrol. **109**: 287–309.

Kent, A.D., Watras, C.J., Eckley, C., Regnell, O., Hintelmann, H., and McMahon, K.D. 2006. Microbial community structure is correlated with mercury methylation in northern Wisconsin lakes. *In* Eighth International Conference on Mercury as a Global Pollutant, 6–11 August 2006, Madison, Wisconsin. UW Sea Grant Program, Madison, Wis. S-1490.

Kolka, R.K., Grigal, D.F., Nater, E.A., and Verry, E.S. 2001. Hydrologic cycling of mercury and organic carbon in a forested upland-bog watershed. Soil Sci. Soc. Am. J. **65**: 897–905.

Krabbenhoft, D.P., and Babiarz, C.L. 1992. The role of groundwater transport in aquatic mercury cycling. Water Resour. Res. **28**(12): 3119–3128.

Lee, Y.H., Bishop, K.H., Munthe, J., Iverfeldt, Å., Verta, M., Parkman, H., and Hultberg, H. 1998. An examination of current Hg deposition and export in Fenno-Scandian catchments. Biogeochemistry, **40**: 125–135.

Lee, Y.H., Bishop, K., and Munthe, J. 2000. Do concepts about catchment cycling of methylmercury and mercury in boreal catchments stand the test of time? Six years of atmospheric inputs and runoff export at Svartberget, northern Sweden. Sci. Total Environ. **260**: 11–20.

Lindqvist, O. 1991. Mercury in the Swedish environment — recent research on causes, consequences and corrective measures. Water Air Soil Pollut. **55**: 1–261.

Magnuson, J.J., Kratz, T.K., and Benson, B.J. (*Editors*). 2006. Long-term dynamics of lakes in the landscape. Oxford University Press, New York.

Mason, R.P., Abbott, M.L., Bodaly, R.A., Bullock, O.R., Driscoll, C.T., Evers, D., Lindberg, S.E., Murray, M., and Swain, E.B. 2005. Monitoring the response to changing mercury deposition. Environ. Sci. Technol. **39**(1): 14A–24A.

Matilainen, T., Verta, M., Korhonen, H., Uusi-Rauva, A., and Neime, M. 2001. Behavior of mercury in soil profiles. Water Air Soil Pollut. **125**: 105–119.

Meili, M. 1991. Mercury in boreal forest lake ecosystems. PhD. thesis, Uppsala Universitat, Uppsala, Sweden.

Meili, M., Bishop, K., Bringmark, L., Johansson, K., Munthe, J., Sverdrup, H., and de Vries, W. 2003. Critical levels of atmospheric pollution: criteria and concepts for operational modelling of mercury in forest and lake ecosystems. Sci. Total Environ. **304**: 83–106.

Mierle, G. 1990. Aqueous inputs of mercury to Precambrian shield lakes in Ontario. Environ. Toxicol. Chem. **9**: 843–851.

Miles, C.J., Moye, H.A., Phlips, E.J., and Sargent, B. 2001. Partitioning of monomethylmercury between freshwater algae and water. Environ. Sci. Technol. **35**(21): 4277–4282.

Miretzky, P., Bisinoti, M.C., and Jardim, W.F. 2005. Sorption of mercury (II) in Amazon soils from column studies. Chemosphere, **60**: 1583–1589.

Moore, T.R., and Dalva, M. 2001. Some controls on the release of dissolved organic carbon by plant tissues and soils. Soil Sci. **166**(1): 38–47.

Morrison, K.A., and Watras, C.J. 1999. Mercury and methyl mercury in freshwater seston: direct determination at picogram per litre levels by dual filtration. Can. J. Fish. Aquat. Sci. **56**(5): 760–766.

Morrison, K.A., Kuhn, E.S., and Watras, C.J. 1995. Comparison of three methods of estimating atmospheric mercury deposition. Environ. Sci. Technol. **29**(3): 571–576.

Moye, H.A., Miles, C.J., Phlips, E.J., Sargent, B., and Merritt, K.K. 2003. Kinetics and uptake mechanisms for monomethylmercury between freshwater algae and water. Environ. Sci. Technol. **36**: 3550–3555.

Nater, E.A., and Grigal, D.F. 1992. Regional trends in mercury deposition across the Great Lakes states, north central USA. Nature (London), **358**: 139–141.

Pickhardt, P.C., and Fisher, N.S. 2007. Accumulation of inorganic and methylmercury by freshwater phytoplankton in two contrasting water bodies. Environ. Sci. Technol. **41**: 125–131.

Porvari, P., Verta, M., Munthe, J., and Haapanen, M. 2003. Forestry practices increase mercury and methylmercury output from boreal forest catchments. Environ. Sci. Technol. **37**: 2389–2393.

Rose, W.J. 1993. Hydrology of Little Rock Lake in Vilas County, north central Wisconsin. US Geological Survey, Madison, Wisconsin, Water Resources Investigations Report No. 93-4139.

Sass, G.G., Kitchell, J.F., Carpenter, S.R., Hrabik, T.R., Marburg, A.E., and Turner, M.G. 2006. Fish community response to a whole-lake removal of coarse woody habitat. Fisheries, **31**(7): 321–330.

Sherman, L.A., Brezonik, P.L., Baker, L.A., and Weir, E.P. 1994. Sediment porewater dynamics of Little Rock Lake, Wisconsin. Limnol. Oceanogr. **39**: 1155–1171.

Skyllberg, U., Qian, J., Frech, W., Xia, K., and Bleam, W.F. 2003. Distribution of mercury, methyl mercury and organic sulphur species in soil, soil solution and streams of a boreal forest catchment. Biogeochemistry, **64**: 53–76.

St. Louis, V.L., Rudd, J.W.M., Kelly, C.A., Beaty, K.G., Flett, R.J., and Roulet, N.T. 1996. Production and loss of methylmercury and loss of total mercury from boreal forest catchments containing different types of wetlands. Environ. Sci. Technol. **30**(9): 2719–2729.

Ullrich, S.M., Tanton, T.W., and Abdrashitova, S.A. 2001. Mercury in the aquatic environment: a review of factors affecting methylation. Crit. Rev. Environ. Sci. Technol. **31**(3): 241–293.

Urban, N.R., and Monte, A.E. 2001. Sulfur burial and loss from the sediments of Little Rock Lake, Wisconsin. Can. J. Fish. Aquat. Sci. **58**: 1347–1355.

Urban, N.R., Sampson, C.J., Brezonik, P.L., and Baker, L.A. 2001. Sulfur cycling in the water column of Little Rock Lake, Wisconsin. Biogeochemistry, **52**: 41–77.

US Environmental Protection Agency. 1996. Method 1669: sampling ambient water for trace metals at EPA water quality criteria levels (EPA 821-R-95-034). Office of Water, Engineering and Analysis Division, Office of Science and Technology, Washington, D.C., EPA 821-R-95-034.

US Environmental Protection Agency. 2001. Method 1630: methyl mercury in water by distillation, aqueous ethylation, purge and trap, and CVAFS (EPA-821-R01-020). Office of Water, Engineering and Analysis Division, Office of Science and Technology, Washington, D.C., EPA-821-R01-020.

US Environmental Protection Agency. 2002. Method 1631, revision E: mercury in water by oxidation, purge and trap, and cold vapor atomic fluorescence spectrometry (EPA 821-R-02-019).

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Office of Water, Engineering and Analysis Division, Office of Science and Technology, Washington, D.C., EPA 821-R-02-019.

Vandal, G.M., Mason, R.P., and Fitzgerald, W.F. 1991. Cycling of volatile mercury in temperate lakes. Water Air Soil Pollut. **56**: 791–803.

Verta, M. 1990. Mercury in Finnish forest lakes and reservoirs: anthropogenic contribution to the load and accumulation in fish. National Board of Waters and the Environment, Helsinki, Finland.

Watras, C.J., Bloom, N.S., Hudson, R.J.M., Gherini, S., Munson, R., Claas, S.A., Morrison, K.A., Hurley, J., Wiener, J.G., Fitzgerald, W.F., Mason, R., Vandal, G., Powell, D., Rada, R., Rislov, L., Winfrey, M., Elder, J., Krabbenhoft, D., Andren, A.W., Babiarz, C., Porcella, D.B., and Huckabee, J.W. 1994. Sources and fates of mercury and methylmercury in Wisconsin lakes. *In* Mercury pollution: integration and synthesis. *Edited by* C.J. Watras and J.W. Huckabee. Lewis Publishers, Chelsea, Michigan. pp. 153–177.

Watras, C.J., Morrison, K.A., Hudson, R.J.M., Frost, T.M., and Kratz, T.K. 2000. Decreasing mercury in northern Wisconsin: temporal patterns in bulk precipitation and a precipitation-dominated lake. Environ. Sci. Technol. **34**(19): 4051–4057.

Watras, C.J., Morrison, K.A., and Kratz, T.K. 2002. Seasonal enrichment and depletion of Hg and SO_4 in Little Rock Lake: relationship to seasonal changes in atmospheric deposition. Can. J. Fish. Aquat. Sci. **59**: 1660–1667.

Watras, C.J., Morrison, K.A., Kent, A., Price, N., Regnell, O., Eckley, C., Hintelmann, H., and Hubacher, T. 2005. Sources of methylmercury to a wetland-dominated lake in northern Wisconsin. Environ. Sci. Technol. **39**(13): 4747–4758.

Watras, C.J., Morrison, K.A., Regnell, O., and Kratz, T.K. 2006. The methylmercury cycle in Little Rock Lake during experimental acidification and recovery. Limnol. Oceanogr. **51**(1): 257–270.

Webster, K.E., Kratz, T.K., Bowser, C.J., and Magnuson, J.J. 1996. The influence of landscape position on lake chemical responses to drought in northern Wisconsin. Limnol. Oceanogr. **41**(5): 977–984.

Wentz, D.A., Rose, W.J., and Webster, K.E. 1995. Long-term hydrologic and biogeochemical responses of a soft water seepage lake in north central Wisconsin. Wat. Resour. Res. **31**(1): 199–212.

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Hierarchical Bayesian modelling with habitat and time covariates for estimating riverine fish population size by successive removal method

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Abstract: We present a hierarchical Bayesian modelling (HBM) framework for estimating riverine fish population size from successive removal data via electrofishing. It is applied to the estimation of the population of Atlantic salmon (*Salmo salar*) juveniles in the Oir River (France). The data set consists of 10 sampling sites sampled by one or two removals over a period of 20 years (1986–2005). We develop and contrast four models to assess the effect of temporal variations and habitat type on the density of fish and the probability of capture. The Bayes factor and the deviance information criterion are used to compare these models. The most credible and parsimonious model is the one that accounts for the effects of the years and the habitat type on the density of fish. It is used to extrapolate the population size in the entire river reach. This paper illustrates that HBM successfully accommodates large but sparse data sets containing poorly informative data for some units. Its conditional structure enables it to borrow strength from data-rich to data-poor units, thus improving the estimations. Predictions of the population size of the entire river reach can be derived, while accounting for all sources of uncertainty.

Résumé : Nous proposons un cadre de modélisation bayésien hiérarchique (HBM) pour estimer l'abondance d'une population de juvéniles de saumon atlantique (*Salmo salar*) dans la rivière Oir (France) par la méthode des retraits successifs par pêche électrique. Le jeu de données est composé de 10 sites d'échantillonnage, chacun ayant été échantillonné par un ou deux passages sur une période de 20 ans (1986–2005). Quatre modèles sont développés pour introduire les variations interannuelles et les effets du type d'habitat sur la densité et sur la probabilité de capture. Ces modèles sont comparés à l'aide du facteur de Bayes et d'un critère d'information basé sur la déviance. Le modèle retenu est celui qui prend en compte l'effet de l'année et du type d'habitat sur la densité de juvéniles de saumons. Il est utilisé pour extrapoler la population de saumon à l'ensemble du cours d'eau. Cet article illustre que les HBM permettent de traiter des jeux de données de grande taille dont l'information portée par chaque unité échantillonnée est hétérogène. La structure conditionnelle permet d'améliorer les estimations car elle organise un transfert d'information entre les unités. Le modèle permet d'obtenir des prédictions de l'abondance sur l'ensemble du cours d'eau, tout en prenant en compte les différentes sources d'incertitude.

Introduction

For fish populations, the quantitative assessment of their abundance is the basis for both scientific research and management. Successive removal by electrofishing is the most commonly used method for deriving estimates of abundance of riverine fish such as salmonids (Bohlin et al. 1989). In Atlantic salmon (*Salmo salar*), the estimation of freshwater juvenile (i.e., parr) abundance is of primary interest. It is critical for the analysis of stock (i.e., egg deposition by spawners) and recruitment (i.e., juvenile production of the subsequent generation) relationships. The transition from the egg to the age-0+ juvenile is a major bottleneck for Atlantic salmon populations (Elliott 2001; Milner et al. 2003). From a management perspective of salmon stocks, the freshwater juvenile is the earliest, the most widely used, and often the sole development stage that can be monitored prior to and independently from fisheries.

Models providing a fair appraisal of the uncertainty about population size estimates are most needed because this uncertainty is relevant to the proper assessment of the uncertainty about population dynamics parameters and ultimately

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the risk associated with management decisions (Harwood and Stokes 2003). State–space modelling is increasingly recommended as a comprehensive and flexible framework for applied population dynamics (Buckland et al. 2004; Clark and Bjørnstad 2004). In a state–space life cycle model like the one developed by Rivot et al. (2004) for Atlantic salmon, a model linking successive removal data to parr abundance can be used as an observation process to update the hidden population renewal process. The present work falls within the perspective of building such an observation model.

For estimating riverine fish population size, the successive removal method is typically used within the context of a two-stage sampling scheme: first, a number of sites are selected from the river stretch of interest and then the fish are sampled from each site by the successive removal method (Hankin 1984; Bohlin et al. 1989). The estimation can be viewed as having two steps: (*i*) estimate population size (or density) at the sampling site level and (*ii*) predict the population on the whole river stretch using these sampling site estimates. In many cases, because of logistic constraints, the proportion of the wetted area sampled is low. As a result, the uncertainty due to the extrapolation process may represent the most important part of the overall uncertainty (Hankin 1984; Mitro and Zale 2000), yet it is often ignored.

Hankin (1984) showed how the data collection should be conducted and how the sampling effort should be allocated in order to optimise the accuracy and precision of the estimation. However, one will often need to retrospectively analyse historical data, possibly collected for a diverse set of objectives. These data rarely fulfil all the conditions required to perform estimation by means of classical methods. Fairly large but sparse data sets are commonplace. The data are often gathered over a rather large number of units, a unit being defined as a sampling site at a given time during the survey. Data of each individual unit may not be informative enough to provide reliable estimates. When the number of fish caught is too small, classical methods may fail or give results with poor precision (Hirst 1994). When only a single pass removal is available, the data do not allow for estimating the catchability parameter. To circumvent these problems, the analyst often has recourse to ad-hoc methods such as crude pooling considering the capture probability is equal for all units or fixing the capture probabilities that cannot be estimated to some values previously estimated from other units (Mitro and Zale 2000). These methods make use of all of the data to confine parameter estimates on the troublesome units, but they ignore, at least partially, the between-unit variability in the unknown quantities and the results of the estimation may be inaccurate or unduly precise (Wyatt 2002). There is a need for a generic, consistent, and robust statistical framework that allows large but sparse data sets to be accommodated, away from "ad-hoceries".

Wyatt (2002, 2003) effectively addressed this issue by a hierarchical Bayesian modelling (HBM) approach applied to the analysis of successive removal data via electrofishing of young-of-the-year (age-0+) juveniles of brown trout (*Salmo trutta*). Hierarchical modelling is one of the most important features of Bayesian data analysis (Gelman et al. 2004). It has been widely applied to the treatment of ecological data (Link et al. 2002; Wikle 2003; Clark 2005), with many applications in the context of fisheries ecology (Harley and Myers 2001; Rivot and Prévost 2002; Michielsen and McAllister 2004). The two companion papers of Wyatt (2002, 2003) explain how the HBM methodology, applied to the combined catch data from all sampling sites in a river stretch, provides better estimates for both the sampled sites and the reach as a whole. The HBM methodology explicitly accounts for the between-site variability in density and capture probability. The founding hypothesis of exchangeable HBM is that the density and the capture probability of each observation unit are drawn, conditionally on covariates, from a common prior probability distribution function (PDF) governed by some unknown parameters. This conditional structure enables information to be shared between units, thus helping to improve the estimation for data-poor units by borrowing strength from data-rich units. Under a Bayesian hierarchical model, obtaining posterior predictive probability distributions for nonsampled units that incorporate the uncertainty resulting from both the sampling error within the sampled sites and the uncertainty due to the variability across units is straightforward. Therefore, estimates of the population size of an entire river reach can be derived while accounting for all sources of uncertainty.

Following the same line of thought, we developed a HBM approach to estimate salmon juvenile population size and apply it the age-0+ parr population of the Oir River (Lower Normandy, France). The available data set is large: 7–10 electrofishing sites sampled over a series of 20 years (1986 to 2005), with typically two successive removals by site. Yet, it is a sparse data set, as the number of fish caught is often very low and there are missing data. Our approach enhances that of Wyatt (2002, 2003) in three significant respects. The first is that we extend it to the joint treatment of multiple years by adding a supplementary level in the hierarchical structure of the models. The second is the introduction of a categorical habitat covariate (instead of a continuous one) to explain the variability of fish density among sampling sites. The third is the assessment of the value of year and habitat type to explain variations in the probability of capture by means of model comparison. We elaborate a baseline model, grounded on well-established prior knowledge about Atlantic salmon juvenile ecology, and further propose three variants of the hierarchical structure by introducing the effects of the year and (or) the habitat type on the probability of capture. We use two Bayesian criteria, the Bayes factor and the deviance information criterion, to compare the four hierarchical structures. These criteria are first used to discard little likely models. We then compare the most credible ones regarding their ultimate objective, i.e., the posterior prediction of total population size. Lastly, we propose a method to extrapolate the results from the sampled sites to the sites not sampled in order to derive an estimation of the population size on the whole stretch of river.

Material and methods

Study site, sampling design, and data

The Oir River is an index river for Atlantic salmon population dynamics and stock assessment in France and Europe

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(Prévost et al. 2003; Baglinière et al. 2005). It is a spawning tributary of the Sélune River, which flows into the English Channel (Fig. 1). It is 19.5 km long with a drainage basin of 85 km^2. A habitat survey covered all the areas colonized by salmon in the Oir River network. Habitat was classified into three categories: rapids–riffles, runs, and pools (Baglinière et al. 1993). Pools were neglected because of the near absence of age-0+ salmon in this type of habitat (Baglinière and Champigneulle 1986) and their marginal occurrence on the Oir River (3.5% of the water surface area). Rapids–riffles and runs are identified based on a combination of depth (<25 cm, between 25 and 60 cm, respectively), water velocity (>40 cm·s^{-1}, between 20 and 40 cm·s^{-1}, respectively), and bottom substrate (a mixture of sand, gravel, and pebbles with a higher proportion of coarse material in the rapid–riffles compared with the runs). Because of the habitat preferences of Atlantic salmon (Bardonnet and Baglinière 2000; Armstrong et al. 2003), this classification has been shown to explain a significant part of the spatial variability of the density of age-0+ juveniles in French rivers (Baglinière and Champigneulle 1986; Dumas and Prouzet 2003).

Since 1986, the age-0+ juvenile production of the main stem was surveyed every year in autumn over a 12.3 km long stretch extending from a trapping facility (the Cerisel Station) to an impassable dam (the Buat Watermill) (Fig. 1). The data are collected according to a two-stage sampling scheme.

For the first stage, depending on the year, 7–10 sampling sites (or inventory sites) were selected within the area of interest (Table 1). Their location is the same every year during the study period, but their surface area may vary between years. Each site is a section of the river associated with a unique habitat type, i.e., rapid–riffle or run. Each sampling unit is identified by three indices i, h, and k: $i = 1,\ldots,20$ for the years 1986 to 2005, respectively; $h = 1, 2$ for the habitat type (rapid–riffle and run, respectively); k stands for the repetition per stratum (i, h) (the number of repetitions varies among strata).

For the second stage, in each unit (i, h, k), the age-0+ salmon population was sampled by electrofishing with two successive removals. From 1986 to 2005, the survey was conducted with a similar operating protocol and essentially the same staff. A direct-current generator (200 W) was used. The fishing crew consisted of three people: the anode operator and two dip-netters. The sites were swept by progressing upstream to surprise the fish, the age-0+ salmon being oriented head upstream. The second pass was realized shortly after the first one. During the experiment, the sampling sites were not closed with barrier nets. However, given the length of the sampling sites (>50 m) and the short lapse of time between consecutive passes, it is considered that immigration into or emigration out of the sampling sites was negligible.

The complete data set consists of the numbers of fish captured at the first and the second pass for 190 sampling units (Table 2). It is a sparse data set because often very small numbers of fish were caught and there are some missing data for the second pass. In the following, it is assumed that the missing data mechanism is ignorable in the sense defined by Gelman et al. (2004). Inferences about the unknowns of the model and the missing data are then carried out without further modelling of the missing data process. The ignorability hypothesis is discussed in detail in Appendix A. The sampling rate (measured as the proportion of the wetted area sampled) in each stratum (i, h) varies between 2.9% and 12.2%.

Baseline model (M_0)

We denote random variables by Greek letters and observed values (i.e., data) and constants by capital letters. $p(\bullet\,|\,\theta)$ denotes a conditional probability distribution function knowing θ. $\bullet|\theta \sim f(\theta)$ means that conditionally on θ, the random variable of interest, has the density f with parameters θ. $E(\bullet)$ is the mean.

Sampling distribution

In electrofishing removal experiments, fish caught at the first pass are removed and are not available to the catch at the second pass. Adhering to the classical assumptions of the removal method (Carle and Strub 1978), for each unit (i, h, k) we assume that (i) the population is closed between the first and the second pass, i.e., no emigration, immigration, recruitment, or natural mortality occur during the experiment; (ii) for each removal event, all the fish have the same probability of capture and are independent from each other with regard to the capture process; and (iii) the probability of capture is constant between the two successive passes. A more realistic model accounting for a decline between the successive pass could have been proposed here. However, because a maximum of two passes is available per site, there would not be much information under our data collection setting to separate out the parameters of such a model, and we would rather choose a more parsimonious option. Based on these assumptions, a binomial model with a constant probability of capture is set to mimic the removal experiments. Catch data of the first and second passes are denoted $C_1(i,h,k)$ and $C_2(i,h,k)$, respectively; $\pi(i,h,k)$ is the probability of capture; and $\nu(i,h,k)$ is the initial population size. The sampling distributions of the catch data are

$$(1a)\quad C_1(i,h,k)\,|\,\nu(i,h,k), \pi(i,h,k) \sim \text{Binomial}(\nu(i,h,k), \pi(i,h,k))$$

$$(1b)\quad C_2(i,h,k)\,|\,C_1(i,h,k), \nu(i,h,k), \pi(i,h,k) \sim \text{Binomial}(\nu(i,h,k) - C_1(i,h,k), \pi(i,h,k))$$

The population size $\nu(i,h,k)$ depends on the expected fish density $\delta(i,h,k)$ (fish·m^{-2}) and the surface area $S(i,h,k)$ of the sampling sites. We assume that the fish are randomly distributed in space within an infinitely large surface from which the site with finite surface $S(i,h,k)$ is randomly picked. Then, $\nu(i,h,k)$ is assumed to be Poisson-distributed with parameter $\lambda(i,h,k) = \delta(i,h,k)\cdot S(i,h,k)$:

$$(2)\quad \nu(i,h,k)\,|\,\lambda(i,h,k) \sim \text{Poisson}(\lambda(i,h,k))$$

Hierarchical structure on δ depending on covariates

Recruitment of age-0+ salmon is known to be highly variable between years. There are potentially many factors causing yearly variations in fish recruitment but they are mostly not identified, uncontrolled, and not monitored (Kennedy and Crozier 1995; Elliott 2001; Milner et al. 2003). Within a

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Fig. 1. The Oir River watershed (France). The section of the Oir River considered in this study appears in bold.

Table 1. Surface area (m^2) of the sampling sites.

	Habitat type 1				Habitat type 2					
Year(s)	1[a]	2	3	4	1	2	3	4	5	6
1986	316	355	666	360	342	—	—	286	—	398
1987	316	355	666	360	342	—	—	286	—	398
1988	340	355	189	164	137	190	111	262	154	131
1989–1998, 2000, 2003–2005	340	355	172	164	137	131	111	262	154	65
1999, 2001	340	355	172	164	137	131	111	262	154	—
2002	340	355	172	—	137	131	111	262	154	—

Note: Habitat types: 1, rapid–riffle; 2, run. Dash (—) indicates that the site was not sampled.
[a]Repetitions (k) 1–4 for habitat type 1 and 1–6 for habitat type 2.

given year, the spatial variability of the density is high and correlated with riverine physical habitat (Amiro 1990; Bardonnet and Baglinière 2000; Armstrong et al. 2003). In French rivers, it has been demonstrated that age-0+ Atlantic salmon densities in autumn where notably higher in rapids–riffles compared with runs (Baglinière and Champigneulle 1986; Dumas and Prouzet 2003; Baglinière et al. 2005).

We incorporate this prior knowledge about the Atlantic salmon ecology by setting a hierarchical structure on the density conditioned by year and habitat type. The densities $\delta(i,h,k)$ are assumed to be partially exchangeable. They are modelled as identically and independently distributed (iid) variables drawn from a lognormal prior PDF. The influence of the covariates year and habitat type is introduced via additive effects on mean log(density) (multiplicative on density). No spatial dependence of the density between adjacent sites is introduced in this model. We denote μ_δ the overall mean of log(density), $\alpha_\delta(i)$ and $\beta_\delta(h)$ the effect of the year i and the habitat h, respectively, and σ^2_δ the between-unit variance that is common to all the (i,h) strata:

$$(3a)\quad E(\log(\delta(i,h))) = \mu_\delta + \alpha_\delta(i) + \beta_\delta(h)$$

$$(3b)\quad \log(\delta(i,h,k))|\mu_\delta, \alpha_\delta(i), \beta_\delta(h), \sigma_\delta \overset{\text{iid}}{\sim} \text{Normal}(E(\log(\delta(i,h,))), \sigma^2_\delta)$$

The years of observation are seen as a sample drawn from an infinite set of years that are exchangeable regarding their effect on density. Thus, conditionally upon between-year variance $\sigma^2_{\alpha_\delta}$, the $\alpha_\delta(i)$s are modelled as random effects, drawn from a common distribution:

$$(4a)\quad \alpha_\delta(i)|\sigma_{\alpha_\delta} \overset{\text{iid}}{\sim} \text{Normal}(0, \sigma^2_{\alpha_\delta})$$

In contrast, the habitat types are a finite and exhaustive set of two mutually exclusive categories and the $\beta_\delta(h)$s are modelled as fixed effects. Consistently with the available knowledge, the $\beta_\delta(h)$s must a priori keep to the constraint $\beta_\delta(1) > \beta_\delta(2)$. To meet this requirement, $\beta_\delta(1)$ is drawn from a half positive normal prior with large variance $V_{\beta_\delta} = 100$, and a

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Table 2. Number of fish captured on the first (C_1) and second (C_2) passes.

	Habitat type 1				Habitat type 2					
Year	1[a]	2	3	4	1	2	3	4	5	6
1986	7, 0	73, 7	37, 4	73, 5	25, 3	—	—	1, 0	—	16, 0
1987	35, 2	23, NS	5, NS	22, 3	15, NS	—	—	0, NS	—	3, NS
1988	3, 0	5, 0	2, 1	20, 1	0, 0	1, 0	3, 0	1, 0	0, 0	0, 0
1989	20, 5	56, 3	6, 1	30, 2	14, 1	0, 0	3, 1	0, NS	2, 1	0, 0
1990	19, 1	54, 4	9, 2	57, 6	11, 1	0, 0	0, 2	2, NS	3, 1	0, 0
1991	28, 3	39, 5	7, 0	14, 1	2, 0	4, 0	1, 0	3, 0	1, 0	0, 1
1992	6, 3	1, 0	1, NS	14, 0	0, 0	0, NS	1, NS	0, 0	0, 0	0, NS
1993	16, 7	2, 1	11, 2	5, 0	0, 0	1, 1	1, 0	1, 0	0, 0	1, 0
1994	5, 1	9, 1	2, NS	3, 0	0, NS	1, NS	0, NS	0, NS	0, NS	0, NS
1995	13, 6	23, 6	17, 2	24, 5	2, NS	1, NS	4, NS	0, NS	0, NS	1, NS
1996	32, 11	15, 2	0, 2	4, 0	8, 0	0, NS	0, 4	1, NS	0, 0	0, NS
1997	79, 13	70, 17	2, 0	50, 6	12, 1	0, NS	4, 1	1, NS	3, NS	0, NS
1998	3, 0	2, 0	0, NS	0, 0	1, 0	0, NS	0, NS	0, NS	0, 0	0, NS
1999	30, 5	12, 1	5, 2	37, 3	7, NS	8, NS	8, NS	1, NS	1, 0	—
2000	27, 7	21, 4	21, 3	36, 10	0, NS	6, NS	19, 3	3, 0	0, NS	11, NS
2001	74, 27	33, 12	21, 1	49, NS	15, 3	3, NS	12, 2	1, NS	4, NS	—
2002	21, 8	25, 15	3, 1	—	0, 0	3, 0	0, 0	0, NS	0, NS	—
2003	31, 4	33, 11	11, 0	62, 12	4, NS	1, NS	16, 2	1, NS	0, NS	2, NS
2004	24, 5	65, 12	2, 0	0, 0	12, 1	0, NS	0, 0	0, NS	3, NS	0, NS
2005	40, 9	45, 12	16, 3	22, 1	6, NS	8, NS	6, NS	0, NS	0, NS	5, NS

Note: Habitat types: 1, rapid–riffle; 2, run. Data are presented as C_1, C_2; NS, second pass not completed. Dash (—) indicates that the site was not sampled at all.

[a]Repetitions (k) 1–4 for habitat 1 and 1–6 for habitat type 2.

sum-to-zero constraint is imposed to avoid confusion with the overall mean μ_β:

$$(4b) \quad \beta_\beta(1) \sim \text{Normal}(0, V_{\beta_0} = 100)I(0,+\infty)$$

and

$$\beta_\beta(2) = -\beta_\beta(1)$$

Exchangeable hierarchical structure on π

The probability of capture $\pi(i,h,k)$ can also vary among units. In stream-dwelling salmonids, many influential factors have been identified (e.g., river width, depth, water velocity, temperature, water conductivity, fish size, habitat complexity), but the results are not fully consistent across studies (Randall 1990; Riley et al. 1993; Speas et al. 2004). In our case study, it is not clear whether the year or the habitat type would a priori cause systematic variations of the probability of capture. Consequently, in the baseline model, a hierarchical structure was used for the probabilities of capture assuming they were fully exchangeable among the sampling units. The logit-transformed probabilities of capture were modelled as identically and independently drawn from a common normal prior PDF with unknown mean μ_π and variance σ_π^2:

$$(5) \quad \text{logit}(\pi(i,h,k))|\mu_\pi,\sigma_\pi \overset{\text{iid}}{\sim} \text{Normal}(\mu_\pi,\sigma_\pi^2)$$

This baseline modelling option is flexible to accommodate variability in the probability of capture, while being parsimonious and allowing a transfer of information between sampling units.

Directed acyclic graph and prior specification

A representation of the baseline model M_0 using the directed acyclic graph (DAG) conventions is provided (Fig. 2). A DAG is a useful metaphor of a Bayesian model that represents the conditional relationship between variables (Spiegelhalter et al. 1996). All the free parameters of the model, i.e., those not conditioned by any quantity, are assigned weakly informative and independent prior PDFs (Table 3). In agreement with Gelman (2006) statement, "we follow the approach of Bernardo (1979) and consider so-called noninformative priors as reference models to be used as a standard of comparison or starting point in place of the proper, informative prior distributions that would be appropriate for a full Bayesian analysis". It is also assumed that the $\pi(i,h,k)$s and the $\delta(i,h,k)$s are a priori uncorrelated. A sensitivity analysis to the choice of priors is presented in Appendix B.

Extended models with effects of the year and the habitat type on π

Because of the uncertainty about systematic effects of the year or the habitat type on the probability of capture, we assessed the value of these covariates to explain variations of the $\pi(i,h,k)$ between sampling units by means of a model comparison. Three variant models were elaborated from M_0 by modifying the hierarchical structure on π.

In the most comprehensive model M_3, the effects of year and habitat type are introduced by means of a partially exchangeable hierarchical structure similar to the one adopted for the densities. We denote μ_π the overall mean of logit(π) and $\alpha_\pi(i)$ and $\beta_\pi(h)$ the effects of year i and habitat h, respectively:

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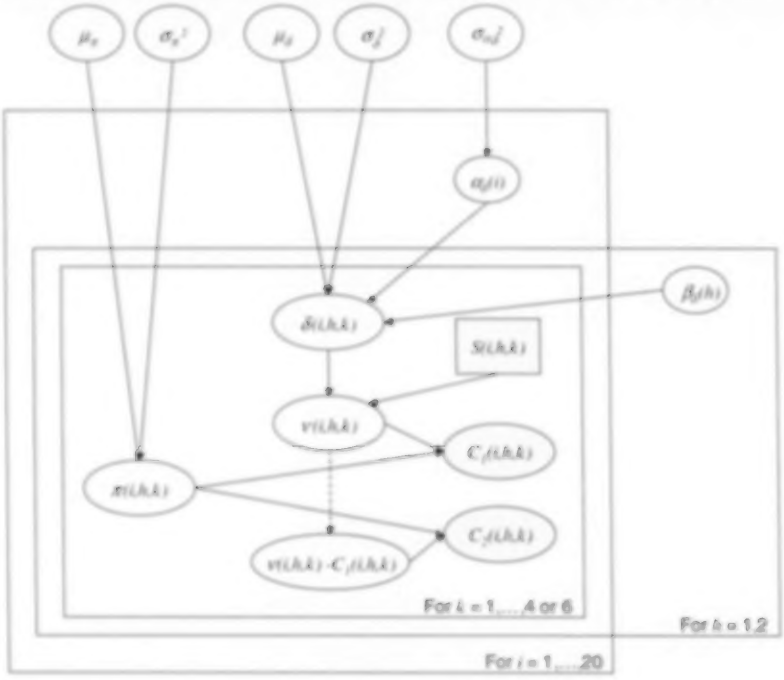
Fig. 2. Directed acyclic graph of the baseline model M_0. Shaded rectangle, known constant; shaded ellipses, observed probabilistic nodes; open ellipses, not observed probabilistic nodes. Arrows indicate the conditional dependencies between nodes: solid arrow, probabilistic dependency; broken arrow, logical dependency. Frame indicates repetition of structure over units.



$$(6a)\quad E(\mathrm{logit}(\pi(i,h))) = \mu_\alpha + \alpha_\alpha(i) + \beta_\beta(h)$$

$$(6b)\quad \mathrm{logit}(\pi(i,h,k))|\mu_\alpha, \alpha_\alpha(i), \beta_\beta(h), \sigma_\alpha \overset{\mathrm{ind}}{\sim} \mathrm{Normal}(E(\mathrm{logit}(\pi(i,h))), \sigma_\alpha^2)$$

The $\alpha_\alpha(i)$s are modelled as random effects (eq. 7*a*). The $\beta_\beta(h)$s are modelled as fixed effects (eq. 7*b*) with a sum-to-zero constraint, but no order is introduced a priori.

$$(7a)\quad \alpha_\alpha(i) \overset{\mathrm{ind}}{\sim} \mathrm{Normal}(0, \sigma_\alpha^2)$$

$$(7b)\quad \beta_\beta(1) \sim \mathrm{Normal}(0, V_{\beta_\beta} = 100) \text{ and } \beta_\beta(2) = -\beta_\beta(1)$$

The two other variant models are nested into M_1 as they only account for the effect of either year (M_1), by setting $\beta_\beta(h) = 0$ for all the habitat types, or habitat (M_2), by setting $\alpha_\alpha(i) = 0$ for all the years. Note that M_0 is also nested within these three variants as it amounts to setting both $\beta_\beta(h) = 0$ and $\alpha_\alpha(i) = 0$. For model M_0, diffuse prior PDFs are used on all parameters (Table 3; a sensitivity analysis to the priors is presented in Appendix B).

Model checking

We used the omnibus χ^2 discrepancy as a summary measure to assess a posteriori the consistency between the model and the data (Gelman et al. 2004, p. 175). We computed the χ^2 statistics for the catch at the two successive passes C_1 and C_2:

$$(8a)\quad \chi^2(C_1, \mathbf{v}, \boldsymbol{\pi}) = \sum_{\text{all units } (i,h,k)=1,\ldots,n} \frac{(C_1(i,h,k) - E(C_1(i,h,k)|\mathbf{v}(i,h,k), \pi(i,h,k)))^2}{\mathrm{Var}(C_1(i,h,k)|\mathbf{v}(i,h,k), \pi(i,h,k))}$$

$$(8b)\quad \chi^2(C_2, \mathbf{v}, \boldsymbol{\pi}) = \sum_{\text{all units } (i,h,k)=1,\ldots,n} \frac{(C_2(i,h,k) - E(C_2(i,h,k)|C_1(i,h,k), \mathbf{v}(i,h,k), \pi(i,h,k)))^2}{\mathrm{Var}(C_2(i,h,k)|C_1(i,h,k), \mathbf{v}(i,h,k), \pi(i,h,k))}$$

For each set of parameters $(\mathbf{v}(i,h,k), \pi(i,h,k))_{i,h,k=1,\ldots,n}$ drawn in their joint posterior distribution, we compared the realized discrepancies $\chi^2(C_1, \mathbf{v}, \boldsymbol{\pi})$ and $\chi^2(C_2, \mathbf{v}, \boldsymbol{\pi})$ computed with the observed values of C_1 and C_2 with the predicted χ^2 discrepancies $\chi^2(C_1^{\mathrm{rep}}, \mathbf{v}, \boldsymbol{\pi})$ and $\chi^2(C_2^{\mathrm{rep}}, \mathbf{v}, \boldsymbol{\pi})$ computed with posterior predictive replicates of C_1 and C_2, $C_1^{\mathrm{rep}}(i,h,k) \sim \mathrm{Binomial}(\mathbf{v}(i,h,k), \pi(i,h,k))$ and $C_2^{\mathrm{rep}}(i,h,k) \sim \mathrm{Binomial}(\mathbf{v}(i,h,k) - C_1(i,h,k), \pi(i,h,k))$. The Bayesian p value is the probability that $\chi^2(C_{\mathrm{pass}}^{\mathrm{rep}}, \mathbf{v}, \boldsymbol{\pi}) \geq \chi^2(C_{\mathrm{pass}}, \mathbf{v}, \boldsymbol{\pi})$ (pass = 1 or 2) estimated over a sample of $(C_{\mathrm{pass}}^{\mathrm{rep}}, \mathbf{v}, \boldsymbol{\pi})$ values. A p value reasonably near 0.5 indicates consistency between the model and the data, whereas very high (near 0.95) or very

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Table 3. Prior distributions of free hyperparameters.

Parameter	Distribution
μ_Δ	~ Normal(0, $V_{0,\Delta}$ = 100)
σ_Δ	~ Uniform on [0, $\sigma_{\Delta,max}$ = 10]
μ_α	~ Normal(0, $V_{0,\alpha}$ = 100)
σ_α	~ Uniform on [0, $\sigma_{\alpha,max}$ = 10]
$\sigma_{\alpha_{ij}}$	~ Uniform on [0, $\sigma_{\alpha_{ij},max}$ = 10]
$\sigma_{\alpha_{ij}}$ (M_1 and M_3 only)	~ Uniform on [0, $\sigma_{\alpha_{ij},max}$ = 10]

Note: All standard deviation parameters σ_Δ, σ_α, $\sigma_{\alpha_{ij}}$, and $\sigma_{\alpha_{ij}}$ are assigned uniform prior on a sufficiently large range, as recommended by Gelman (2006) for hierarchical models.

low (near 0.05) p values provide serious warning. In order to check for inconsistencies for particular years or habitat type, these calculations were also done by restricting the sums in eqs. 8*a* and 8*b* to the year or habitat type of interest.

Model comparison by means of Bayes factor and deviance information criterion

The Bayes factor $BF_{i,j}$ is a measure of the relative credibility of the model M_i compared with the model M_j given the data (Kass and Raftery 1995). It is defined as the ratio of the marginal likelihood under the model M_i to the marginal likelihood under the model M_j:

$$(9a) \quad BF_{i,j} = \frac{L_{M_i}(\text{DATA})}{L_{M_j}(\text{DATA})}$$

$$(9b) \quad L_{M_i}(\text{DATA}) = \int_{\theta} p(\text{DATA}|\theta) p(\theta) d\theta$$

i.e., the ratio of the posterior probability of the two models when their prior probabilities are equal. We used the method proposed by Kass and Raftery (1995) to approximate the marginal likelihood by the posterior harmonic mean of the likelihood calculated over a sample drawn from the posterior PDF of the set of parameters θ:

$$(9c) \quad \hat{L}_M(\text{DATA}) = \left(\frac{1}{G} \sum_{g=1}^{G} L_M(\text{DATA}, \theta^{(g)})^{-1} \right)^{-1}$$

where $\theta^{(g)}$ is the gth set of parameters of the sample, $L_M(\text{DATA}, \theta^{(g)})$ is the value of the sampling density of the observed data in the model M calculated at $\theta^{(g)}$, and G is the sample size. This estimate of the marginal likelihood may be unstable, because the harmonic mean of the likelihood is highly sensitive to the very small values of the likelihood that may appear during the sampling. This may hinder the comparison of two models when their difference in credibility is low. If the contrast between the credibility of the different models is high, the approximation from eq. 9*c* gives results that are accurate enough for identifying the most credible model(s).

The deviance information criterion (DIC; Spiegelhalter et al. 2002) is a measure of complexity and fit designed to compare hierarchical models of arbitrary structure. Its rationale and interpretation are different than these of the BF and are more analogue to the frequentist Akaike information criterion (AIC): the smaller the DIC, the more favoured is a model. It combines a measure of the goodness of fit, defined as the posterior mean of the deviance $\overline{\text{Dev}(\theta)}$ (where the deviance is −2 times the log-likelihood), with a measure of the model complexity pD, acting as a penalty term:

$$(10) \quad \text{DIC} = \overline{\text{Dev}(\theta)} + pD$$

pD is defined as $pD = \overline{\text{Dev}(\theta)} - \text{Dev}(\hat{\theta})$, where $\hat{\theta}$ is a point estimate of the parameter vector. The posterior mean is the natural choice for $\hat{\theta}$. However, following Spiegelhalter et al. (2002), we used the posterior medians instead because they are better point estimates when the posterior densities of the parameters are highly skewed. The DIC is easily calculated by sampling techniques and its computation avoids the instability observed when estimating BF from eq. 9*c*.

The BF is known to be sensitive to the prior choice. To assess this sensitivity, we fit and compared the four models $M_0, \ldots, M_3$ under alternative prior configurations (see Appendix B).

Extrapolation to the whole river stretch

The ultimate goal of our study is to provide estimates of the total age-0+ salmon population for each year i, denoted $N(i)$. It is the sum of the population size $N_s(i)$ estimated on the sampling sites with the population size $N_e(i)$ predicted on the nonsampled area, where $N_s(i)$ and $N_e(i)$ are calculated as a sum over the habitat types:

$$(11) \quad N(i) = \sum_{h=1}^{2} N_s(i,h) + \sum_{h=1}^{2} N_e(i,h)$$

Each term $N_s(i,h)$ is directly issued from the model under concern (M_0 to M_3). It is the sum of the estimated population size $N(i,h,k)$ over all the sampling units with habitat type h. The $N_e(i,h)$ are the extrapolated population sizes for the (i,h) strata.

The relative importance of the extrapolation term $N_e(i)$ depends on the sampling rate. At one extreme, if the whole water surface area was sampled, then $N_e(i) = 0$. At the other extreme, if a very small proportion of the water surface area was sampled, then $N_e(i)$ makes up a very high proportion of $N(i)$. Two sources of uncertainty, corresponding to the two stages of the sampling scheme, must be taken into account in the estimation of $N(i)$: that arising from the binomial sampling errors associated with the removal method within the sampling units and that arising from the sampling variance between the sampling units. The second source of uncertainty concerns the extrapolation term $N_e(i)$ only. It depends on the sampling rate and on the spatial variability of the density. If the sampling rate is low and the density is highly variable, it can represent the greatest source of uncertainty in the estimation of $N(i)$.

To explicitly account for spatial variability in density within the (i,h) strata, we mimic the first stage of the sampling scheme: the whole river is regarded as being divided into a very large number of sites (sufficiently large to be considered as infinite) from which the sampled sites were drawn. The nonsampled surface area $S_e(i,h)$ (Table 4) is considered to consist of a number $n_e(i,h)$ of sites of equal surface area $S_e^*(i,h)$. $n_e(i,h)$ is set so that $S_e^*(i,h)$ is approxi-

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Table 4. Sampled and unsampled (extrapolation) surface area (m²) by habitat types 1 and 2.

	$S_s(i,h)$		$\bar{S}_s(i,h)$		$S_e(i,h)$		$n_e(i,h)$		$S_e^2(i,h)$	
Years	1	2	1	2	1	2	1	2	1	2
1986, 1987	1697	1026	424	342	12181	26078	29	76	420	343
1988	1048	985	262	164	12830	26119	49	159	262	164
1989–1998, 2000, 2003–2005	1031	860	258	143	12847	26244	50	183	257	143
1999, 2001	1031	795	258	159	12847	26309	50	165	257	159
2002	867	795	289	159	13011	26309	45	165	289	159
2003–2005	1031	860	258	143	12847	26244	50	183	257	143

Note: $S_s(i,h)$, total sampled area in year i and habitat type h; $\bar{S}_s(i,h)$, mean area of sampling sites; $S_e(i,h)$, extrapolation area; $n_e(i,h)$, number of sites for the extrapolation; $S_e^2(i,h)$, area of the extrapolation sites. Habitat types: 1, rapids–riffles; 2, runs. Total surface area of the river by habitat type: 1, 13 878 m²; 2, 27 104 m².

mately equal to the mean surface of the sampled sites $\bar{S}_s(i,h)$:

$$(12)\quad n_e(i,h) = \mathrm{int}\left(\frac{S_e(i,h)}{\bar{S}_s(i,h)}\right) \quad \text{and} \quad S_e^2(i,h) = \frac{S_e(i,h)}{n_e(i,h)}$$

According to the conditional structure of our models, the densities $\delta_e^2(i,h,l)$ at the nonsampled sites $l = 1,\ldots,n_e(i,h)$ are identically distributed according to

$$(13)\quad p(\delta_e^2(i,h,l)|\mathrm{DATA}) = \int p(\delta_e^2(i,h,l)|\theta_\delta(i,h)) \times p(\theta_\delta(i,h)|\mathrm{DATA})\mathrm{d}(\theta_\delta(i,h))$$

where $\theta_\delta(i,h) = (\mu_\delta, \alpha_\delta(i), \beta_\delta(h), \sigma_\delta)$. This PDF is formed by two terms: the first one is the conditional distribution of the density given the parameters $\theta_\delta(i,h)$ and reflects the uncertainty due to between-unit spatial variability of the density in the stratum (i,h) and the second one is the joint posterior distribution of $\theta_\delta(i,h)$, which conveys the uncertainty of the mean density for the (i,h) stratum considered. Given the densities $\delta_e^2(i,h,l)$, the population sizes $v_e^2(i,h,l)$ are iid:

$$(14)\quad v_e^2(i,h,l)|\delta_e^2(i,h,l), S_e^2(i,h) \overset{iid}{\sim} \mathrm{Poisson}(\delta_e^2(i,h,l) \times S_e^2(i,h))$$

The population size of the nonsampled area in the (i,h) stratum is then

$$(15)\quad v_e(i,h) = \sum_{l=1}^{n_e(i,h)} v_e^2(i,h,l)$$

Bayesian computations

In our data set, some of the catch data C_2 are missing. Assuming that they are missing at random, their treatment in the Bayesian setting is straightforward and can be done by data-augmentation techniques (Gelman et al. 2004). The missing data are considered as any other unknown quantity of a model. Posterior inference about any set of unknowns of interest is obtained by integrating over the posterior PDF of the missing data. The uncertainty inherent to the missing data is then taken into account. Such an integration is painless when sampling methods are used to derive the posterior inferences.

We performed all the posterior inferences using Markov chain Monte Carlo (MCMC) sampling. MCMC methods now enable the Bayesian estimation of complex highly dimensional hierarchical models, which could not be treated otherwise (Brooks 2003). MCMC sampling was carried out by means of the WinBUGS® software (Spiegelhalter et al. 2003) and the BRugs package of R (www.r-project.org). It was used to obtain a sample from the joint posterior distribution of all unknowns, i.e., model parameters, missing data, and predictions. The convergence of the MCMC chains to their ergodic distribution was tested for the model parameters via the Gelman–Rubin (GR) diagnostics as implemented by WinBUGS®. This diagnostic assesses the mixing of several independent chains starting at contrasted initial values spread over the variable space. We used three independent chains, and the first 10 000 iterations were discarded as an initial burn-in period. Then, 100 000 further iterations were performed and convergence was checked using the GR diagnostic. CPU time needed to run three parallel chains is 1 h with a 2.8GHz Intel P4 processor. All inferences were derived using the sample obtained from pooling the three chains (i.e., size = 300 000). To smooth the numeric instability in the computation of the BF, a sample of size 600 000 was used to compute BF.

Results

The outcomes of the model comparison and the posterior estimation are robust to the choice of the prior configuration (see Appendix B). The results presented in the following are those obtained under the baseline prior configuration described in the Material and methods section.

Model comparison

Both models M_2 and M_3 are clearly discarded by the BF (Table 5). Based on the guidelines proposed by Kass and Raftery (1995) for interpreting BF values, the evidence against M_2 and M_3 is very strong and there is slightly less support for M_1 compared with M_0. These results are robust against the instability of the BF approximations calculated by the Kass and Raftery (1995) method (Appendix B). The differences between the DIC values of the four models are much less contrasted (Table 5). To interpret DIC values, Spiegelhalter et al. (2002) suggest adopting the rule of thumb proposed by Burnham and Anderson (2002) for AIC. Following this, none of the four models can be clearly discarded. Given these results, we retained M_0 as the preferred model, with M_1 as a valuable alternative candidate.

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Table 5. Alternative competing models and criterions for model selection.

	Effects introduced in the model							
	Density		Probability of capture					
Models	Year	Habitat	Year	Habitat	$\overline{\text{Dev}(\theta)}$	*pD*	DIC	Log(BF M_0 vs. M_i)
M_0	×	×	—	—	576	239	815	0
M_1	×	×	×	—	586	231	817	1.2
M_2	×	×	—	×	574	240	814	3.7
M_3	×	×	×	×	584	230	814	5.6

Note: Values are computed under the baseline prior configuration as described in the Material and methods section. ×, the effect of the corresponding covariate is introduced; —, no effect is introduced. $\overline{\text{Dev}(\theta)}$, the posterior mean of the deviance; *pD*, measure of the model complexity; DIC, deviance information criterion; BF, Bayes factors. BFs are estimated from eqs. 9*a*–9*c* by considering the whole Markov chain Monte Carlo (MCMC) sample (size = 600 000); M_i, model *i*, *i* = 1–3; M_0, baseline model.

Table 6. Main statistics of the marginal posterior probability distribution functions (PDFs) of the free parameters in model M_0.

	Mean	SD	2.5%	5%	25%	Median	75%	95%	97.5%
μ_δ	0.87	0.25	0.37	0.46	0.71	0.87	1.03	1.27	1.35
σ_δ	1.09	0.09	0.93	0.95	1.03	1.09	1.15	1.25	1.29
μ_π	1.62	0.11	1.41	1.44	1.55	1.62	1.70	1.81	1.85
σ_π	0.61	0.13	0.37	0.41	0.52	0.60	0.69	0.84	0.89
σ_{α_δ}	0.97	0.22	0.63	0.67	0.82	0.95	1.10	1.36	1.47

Note: Posterior PDFs are computed under the baseline prior configuration as described in the Material and methods section. All statistics are computed from a Markov chain Monte Carlo (MCMC) sample (size = 300 000). SD, standard deviation.

Estimation

Model M_0

The estimation of the overall mean density in the log scale (μ_δ) is fairly precise (Table 6). The posterior PDFs of the $\alpha_\delta(i)$s (Fig. 3*a*) illustrate the high between-year variability of the age-0+ salmon density without any particular trend. The variability between the $\alpha_\delta(i)$s (the mean of the posterior PDF of σ_{α_δ} is 0.97; Table 6) is much higher than the within-year uncertainty of estimated effects (the standard deviations of the posterior PDF of the $\alpha_\delta(i)$s range from 0.42 to 0.58 according to the year). In the natural scale of the density, the mean of the posterior predictive PDFs of the density on a rapid–riffle habitat in a given year ranges from 0.018 (year 1998) to 0.38 fish·m^{-2} (year 2001). The effect of the habitat type on the density is very strong (Fig. 3*b*). The mean of the posterior PDF of the density ratio in the habitat type 1 versus type 2, calculated as $e^{\beta_\delta(1)}/e^{\beta_\delta(2)}$, is 6.5. Even after accounting for the effects of year and habitat type, the residual spatial variability of the density σ_δ remains high when compared with the overall mean μ_δ or with the between-year variability σ_{α_δ} (Table 6).

The overall mean probability of capture in the logit scale, μ_π, is estimated with good precision (Table 6). In the natural scale, the mean of the posterior predictive PDF of the probability of capture is 0.82. The between-unit variability of the probability of capture (σ_π) is rather low compared with the overall mean μ_π (Table 6). Consistently, even for units with missing or little informative data, the probability of capture is rather precisely estimated (the $\pi(i,h,k)$ have dome-shaped posterior densities close to 0 around 0 and 1) and rather high (the mean of the posterior PDF of the probability of capture ranges from 0.64 to 0.90 according to the sampling unit).

Model M_1

The between-year variability of the probability of capture, as illustrated by the posterior PDFs of the $\alpha_\pi(i)$s (Fig. 3*c*), is significant but with no particular pattern. In the natural scale of the probability of capture, the mean of the posterior predictive PDF of the probability of capture in a given year ranges from 0.68 (2002) to 0.9 (1986). The posterior PDFs of the $\alpha_\delta(i)$s (not shown) are very similar to those obtained from the model M_0. There is no evidence of confusion between the effects of year on the density and on the probability of capture. The patterns of the between-year variations of the estimated effects $\alpha_\delta(i)$s and $\alpha_\pi(i)$s are different, and the joint posterior PDFs of each couple $(\alpha_\delta(i),\alpha_\pi(i))$ (not shown) do not reveal any noteworthy correlation pattern.

Models M_2 and M_3

For both models there is no significant effect of habitat type on the probability of capture (Figs. 3*d* and 3*f*). The year effect on the probability of capture from the model M_3 (Fig. 3*e*) is similar to that obtained from the model M_1 (Fig. 3*c*).

Model checking

We only report the results of the posterior checking obtained for our favourite model M_0. The plots of the χ^2 discrepancy statistics do not reveal any significant inconsistency between M_0 and the data (Fig. 4). The *p* values of 0.28 (first pass) and 0.55 (second pass) indicate that the discrepancies

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Fig. 3. Summaries of the marginal posterior probability distribution functions (PDFs) of (*a*) the $\alpha_0(i)$s under the baseline model M_0, (*b*) the $\beta_0(h)$s under M_0, (*c*) the $\alpha_1(i)$s under model M_1, (*d*) the $\beta_0(h)$s under model M_2, (*e*) the $\alpha_2(i)$s under model M_3, and (*f*) the $\beta_2(h)$s under model M_3. Posterior PDFs are computed under the baseline prior configuration as described in the Material and methods section. Median (solid circle), 25% and 75% percentiles (solid triangles), and 5% and 95% percentile (+) are computed from a Markov chain Monte Carlo (MCMC) sample (size = 300 000).

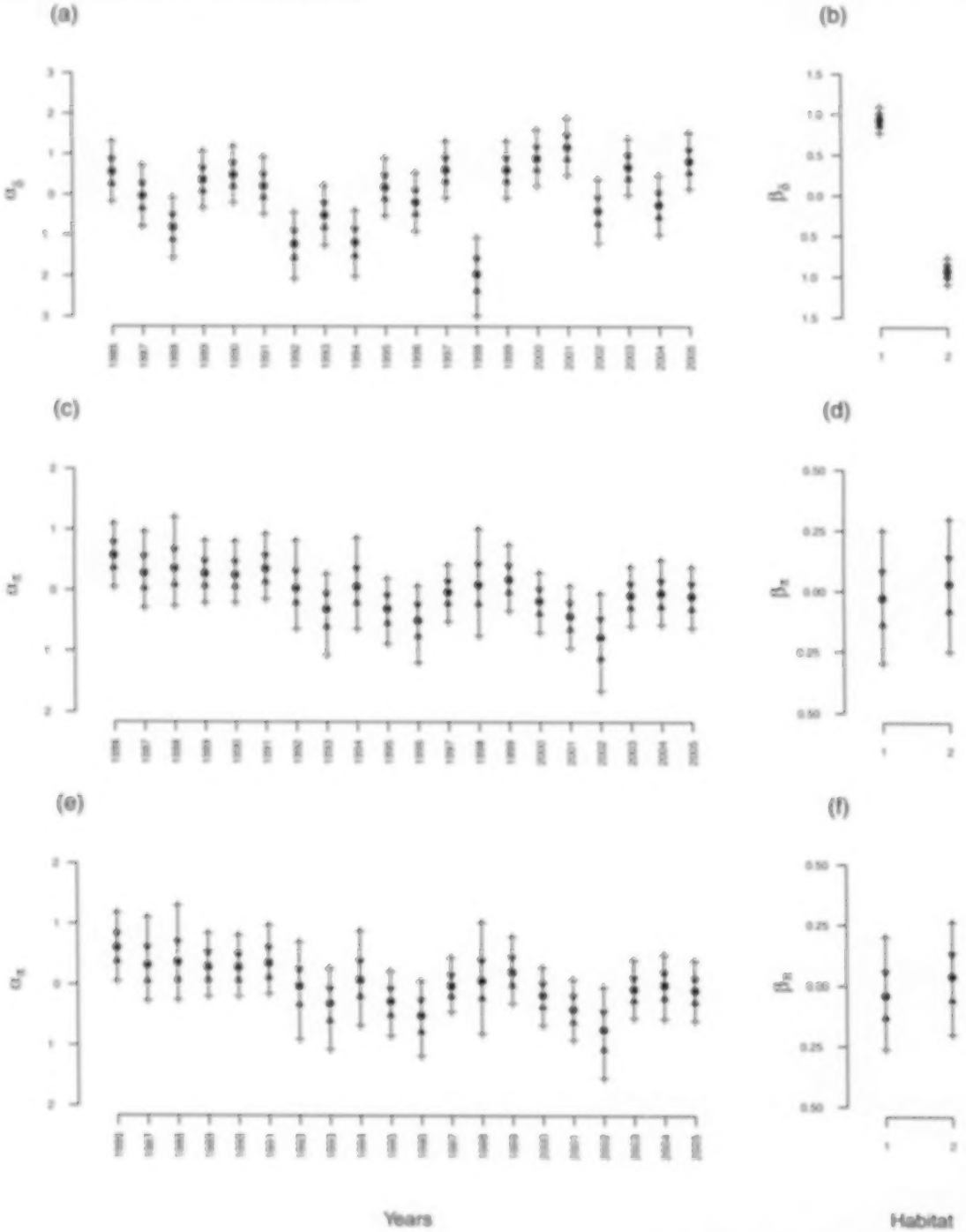

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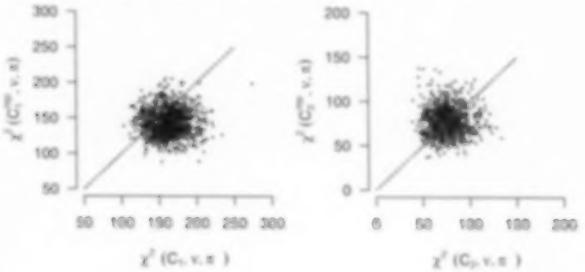
Fig. 4. Discrepancy plot obtained from the baseline model M_0. $\chi^2(C_1,\nu,\pi)$ and $\chi^2(C_2,\nu,\pi)$ are the realized discrepancies computed with the observed values of C_1 and C_2. $\chi^2(C_1^{rep},\nu,\pi)$ and $\chi^2(C_2^{rep},\nu,\pi)$ are the predicted discrepancies computed with posterior predictive replicates C_1^{rep} and C_2^{rep}. The corresponding p values are 0.28 and 0.55.



calculated from the observed C_1 and C_2 are not systematically different from discrepancies calculated from the a posteriori predicted C_1^{rep} and C_2^{rep} values. The p values computed per year range from 0.18 to 0.67 (first pass) and from 0.37 to 0.84 (second pass). The p values computed per habitat type are 0.22 and 0.47 (first pass) and 0.51 and 0.63 (second pass). They do not indicate any major flaw either.

Extrapolation to the whole river stretch

Given the results of the model comparison, both M_0 and M_1 were used to estimate the population size on the whole river stretch. The posterior predictive PDFs of the $v(i)$s (eqs. 11*a*–11*b*) are almost identical in terms of both expected values and precision, whether model M_0 or M_1 is used (Fig. 5). We then eventually retain the most parsimonious one, M_0, as our preferred model.

The between-year variability of the estimated population size is high with no particular trend (Fig. 5). The posterior mean of $v(i)$ ranges from 309 (year 1998) to 6762 (year 2001). The contrast in the uncertainty about the yearly population size estimates is large as well. As expected when using lognormal distributions for the densities, the uncertainty about the population size estimates increases with their means.

The estimates of the age-0+ population size (posterior means of the $v(i)$s, years 1986–2003) were compared with those of the smolt run (from capture–mark–recapture data) of the corresponding cohorts provided by Baglinière et al. (2005) (Fig. 6). The correlation between the two estimates is consistent with moderate yearly fluctuations of the age-0+–smolt survival rate in the Oir River.

Discussion

Critical examination of modelling hypotheses

The accuracy of the model used for the removal method in each sampling unit depends on the fulfilment of its basic assumptions: (*i*) change in population size only occurs through the capture process; (*ii*) during each removal pass, the fish are identically and independently distributed with regard to the probability of capture; and (*iii*) the probability of capture is constant between the first and the second removal pass. Certainly the last hypothesis is the most questionable. Indeed, the probability of capture is likely to decrease in successive removals (Bohlin and Cowx 1990; Peterson et al. 2004). This has been suggested to arise from different

Fig. 5. Summaries of the marginal posterior probability distribution functions (PDFs) of the total age-0+ salmon population size obtained from models M_0 and M_1. Posterior PDFs are computed under the baseline prior configuration as described in the Material and methods section. For each year (x axis), the posterior distributions obtained from M_0 (left) and M_1 (right) are presented. Mean (open square), median (solid circle), the 25% and 75% percentiles (solid triangles), and the 5% and 95% percentiles (+) are computed from a Markov chain Monte Carlo (MCMC) sample (size = 300 000).

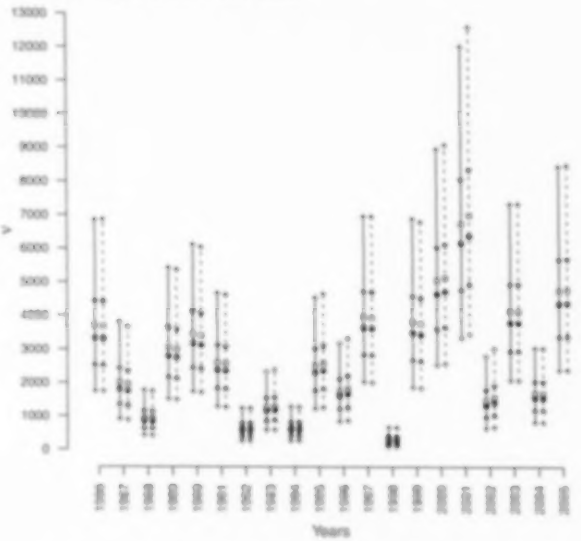
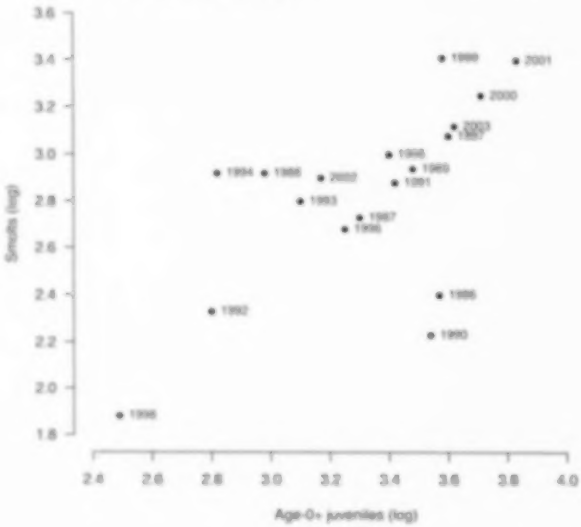


Fig. 6. Estimates of the smolt run size by cohort (from capture–mark–recapture data; Baglinière et al. 2005) plotted against the corresponding age-0+ population size (posterior means of the $v(i)$s, years 1986–2003) estimates.



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causes: (*i*) heterogeneous catchability among individuals, leading to the most easily captured individuals being caught first (Dolan and Miranda 2003; Mäntyniemi et al. 2005); (*ii*) a decrease in catchability between successive passes due to changes in the fish behaviour or the reduced susceptibility to electricity for fish already having experienced an electric shock (Bohlin et al. 1990). Schnute (1983) proposed a more realistic approach that allows for a decline in the probability of capture between passes. Wang and Loneragan (1996) developed an overdispersed model where the probability of capture varies randomly and independently among passes. Mäntyniemi et al. (2005) proposed a model explicitly accounting for a random between-individual variability in the probability of capture. Following these authors, more realistic models could have been applied to the data. However, there is not much information about the parameters of such models when only two passes are available. Using such a model would have required the use of informative priors to avoid confusion among parameters in the posterior inferences. The use of informative priors is fine in theory but has to be taken with great caution in practice. Informative priors should be derived from existing information (i.e., data or expert opinion) by formal means (e.g., meta-analysis or formal methods for prior elicitation from expert opinion) and by a thorough examination of all the sources of information available. Otherwise, there is a great risk that the practitioner, even unintentionally, favours his own beliefs over alternatives. In addition, when the modeller also has a good knowledge of the observed data available for the Bayesian updating, it is very difficult to elaborate informative priors independently from this knowledge, with the undesired consequence of using part of the information of the data twice. Hence, without dismissing the ultimate interest in using informative priors and complex models, an analysis based on parsimonious models with vague reference priors was our preferred default approach. As a first step, it is useful — would it only be for an illustrative purpose — to ensure that the posterior estimates reflect primarily the information contained in the data (Gelman et al. 2004; Gelman 2006). For this reason, we built a simplified model where the capture probability is constant between the two successive passes. Still, our results depend on this hypothesis. Our simplification is likely to cause not only underestimation of the population size (Peterson et al. 2004; Mäntyniemi et al. 2005; Rosenberg and Dunhman 2005), but also underestimation of the uncertainty and overestimation of spatiotemporal variability (Mäntyniemi et al. 2005). In our case, this problems may not be too acute. Indeed, the probability of capture is high (on average from 0.68 to 0.9 according to the year). In addition, the age-0+ salmon juveniles are mainly found in open shallow waters in the middle of the river channel and their size range is limited. These conditions favour robustness against the violation of the constant catchability hypothesis (Mäntyniemi et al. 2005).

Fish densities have been assumed to be lognormally distributed. We did not formally test for the relevance of this modelling hypothesis, which is both convenient and classical. It allows the introduction of multiplicative effects of covariates on the density by means of standard linear-normal modelling of the log(density). The commonly held belief that population abundance follows a lognormal distribution has been critically examined by Halley and Inchausti (2002). These authors recommend the gamma PDF as the most valuable alternative. Our HBM approach could readily be adapted to gamma-distributed fish densities. Using the scale–shape parameterisation of the gamma PDF, it is easy to introduce multiplicative effects of covariates on the mean.

For the sake of simplicity, no spatial dependence between densities at adjacent sites was introduced. We focussed our modelling effort on the joint treatment of several years and the accounting for habitat effects. Further development of spatially structured models is certainly warranted as it has been demonstrated that juvenile salmon densities are spatially autocorrelated (De Oliveira et al. 2001). The spatially explicit model coupled with a GIS developed by Wyatt (2003) is an interesting starting point in that direction.

Under our HBM approach, priors have to be assigned to the hyperparameters at the top of the multilevel structure. One could have looked for hyperpriors that would better reflect our prior knowledge about the spatial and temporal variability of the density and the probability of capture. However, we instead used weakly informative priors. This choice was motivated by arguments already discussed. Still, strong prior knowledge about the spatial variability of the densities is introduced in the hierarchical model structure through (*i*) the definition of habitat covariates and (*ii*) the constraints that we imposed on the habitat effects for the density (we imposed $\beta_3(h = 1) > \beta_3(h = 2)$, where $\beta_3(h = 1)$ and $\beta_3(h = 2)$ represent the effects of rapid–riffle habitat and run habitat on the density, respectively).

Bayesian tools for model comparison

We jointly used the BF and the DIC to compare our four competing models. In the Bayesian framework, the BF is a natural tool to compare the relative credibility of alternative models, yet it is not often implemented. It suffers from two main drawbacks: it may be difficult to calculate, and it may be highly sensitive to the prior. Yet, it revealed a valuable operational tool in our case. Among the various MCMC methods available to compute the BF, the "product space search" method or the "reversible jump" algorithm (reviewed in Han and Carlin 2001) are more recommended but are difficult to put into practice when more than two competing models are compared. We estimated the BF values from a simple method based on a MCMC integration of the likelihood (Kass and Raftery 1995). The numerical instability of this technique did not preclude the identification of the most credible model because the magnitude of the instability was much lower than the BF itself (Appendix B). We contrasted various prior configurations to assess the sensitivity of the BF. Because our data set is informative enough, the conclusion drawn from the BF was revealed to be robust to these prior hypotheses (Appendix B).

The DIC is more recent and its application for model selection is still being discussed (Spiegelhalter et al. 2002; Celeux et al. 2006). This criterion is appealing because of its straightforward computation from posterior samples and its numerical stability, but its rationale and interpretation are different than those of the BF. The differences between the DIC values of the four models were much less contrasted than BF values, and none of the four models could clearly be discarded based on this criterion. The results seem to con-

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firm the general tendency of the BF to opt for more parsimonious models compared with other model selection tools such as AIC, an analogue to the DIC in its construction and its interpretation (Kass and Raftery 1995).

In a full Bayesian approach for estimating the population in the entire river stretch, we could have undertaken Bayesian model averaging (BMA) to account for model uncertainty (Hoeting et al. 1999; King and Brooks 2001). Posterior estimations would have been obtained by averaging the posterior PDFs derived from the alternative models, with the posterior relative credibility of each model as weights. The posterior relative credibility is easily derived from the BF. In our case study, the clearly discarded models M_2 and M_3 are not worth considering in a BMA approach as their weights would be so small that they would not effectively contribute to the averaging procedure. Under the hypothesis of a prior odd of 1 between the two most likely models M_0 and M_1, their relative credibilities are 0.77 and 0.23, respectively. However, our results proved that both models lead to very similar estimations (Fig. 4). Implementing a time-consuming and computationally intensive BMA approach would have been a distraction, and we recommend the single use of the most parsimonious model M_0.

A powerful and flexible framework for integrating successive removal data

The HBM framework proved powerful and flexible for processing multiyear and multisite successive removal data. It successfully enabled joint treatment of several years of data and integration of a habitat-categorical covariate explaining part of the spatial variability of the density of salmon juveniles. Our modelling approach takes advantage of the "borrowing of strength" between units and the additional information brought by the habitat covariate to improve the estimation of the total salmon population size every year.

The HBM framework successfully accommodated our large but sparse data set, which contained poorly informative or even missing data for some units. The conditional probability structure enables the transfer of information from data-rich to data-poor units, while explicitly accounting for the cross-units variability of the density and probability of capture. The posterior predictive PDF of the probability of capture conveys all the posterior information that can be used to infer the density at any site where only one pass is carried out. This methodology is more comprehensive compared with others (e.g., the mean capture probability method; Mitro and Zale 2000) that only address the transfer of information issue in a rather ad-hoc manner. This method could be taken advantage of to enhance the precision of the yearly population size estimates without augmenting the sampling effort. The sampling area could be increased by reallocating part of the sampling effort to additional single removal sites. Such strategy would be of special interest when the between-site variability of the density represents the main source of uncertainty, as is often the case (Hankin 1984; Mitro and Zale 2000).

Our HBM approach provides estimates of the population size on a whole river stretch, while accounting for the two sources of uncertainty associated with the two-stage sampling scheme: (*i*) the sampling variance due to the removal method in sampling sites and (*ii*) the uncertainty arising from the across-site variability of the density. The resulting posterior PDF of the population size can be used in further stock assessment work or population dynamics studies.

Improving the assessment of population size and dynamics

The results obtained from our case study are sensible, consistent, and insightful for the dynamics and the management of Atlantic salmon populations. They highlight that the probability of capture varies among units. Several factors, both abiotic (e.g., river width, depth, water velocity, temperature, water conductivity, habitat complexity) and biotic (e.g., fish size, fish density), could explain this variability (Randall 1990; Riley et al. 1993; Speas et al. 2004). Systematic variations of these variables may translate into an effect of the year and the habitat type, but our results indicate that once the influence of these covariates on the density has been taken into account, there is no significant effect of habitat type on the probability of capture. This can be explained by two facts: (*i*) in spite of the variability of the salmon habitat, many physical characteristics of the stream remain relatively homogeneous along the stretch of interest and (*ii*) the electrofishing crew is trained to operate in a consistent manner to maximise the capture efficiency whatever the habitat type. Conclusions regarding the effect of the year on the probability of capture are less clear-cut. Indeed, the BF is in favour of M_0 (no effect of years), whereas the DIC is in favour of M_1 (effect of year), and the posterior estimates of the $\alpha_p(i)$s suggest that year effects may be significant. Variations of the hydrological conditions between years during the electrofishing campaigns may explain part of the observed pattern.

The age-0+ salmon density fluctuates widely between years. This is a typical result for juvenile salmonid recruitment, which is highly sensitive to environmental fluctuations (Elliott 2001; Milner et al. 2003; Baglinière et al. 2005). On average, the density of age-0+ juveniles on rapid–riffle habitat is 6.5 times higher than on run habitat. These figures are in agreement with previous findings on the habitat preferences of Atlantic salmon (Bardonnet and Baglinière 2000; Armstrong et al. 2003) and with interhabitat ratios established for French rivers (Baglinière et al. 2005). We also show that our estimates of the age-0+ population size are well correlated with those of the smolt run of the corresponding cohorts, which is consistent with previous knowledge about the low yearly fluctuations of the age-0+–smolt survival rates in French rivers.

Fish density was extrapolated over 95% of the study area. Because the spatial variability of the density is high, a high price is paid in terms of uncertainty for the very low sampling rate, and our estimates of the population size have poor precision. By the sole use of the available electrofishing data, only very large variations in the population size can be detected, but our HBM framework for the estimation of age-0+ population size can also serve to incorporate information into a population dynamic model. Rivot et al. (2004) illustrated the coupling of capture–mark–recapture observation models with a population dynamics life cycle model for Atlantic salmon, within the Bayesian state–space modelling framework. This flexible methodology can accommodate an additional observation model to assimilate the successive removal data on juveniles into the population dynamics model

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and, therefore, improve the estimation of demographic parameters and the predictions about the future of the population.

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References

Amiro, P.G. 1990. Variation in juvenile Atlantic salmon population densities between consecutive enclosed sections of streams. *In* Development in electric fishing. *Edited by* I.G. Cowx. Fishing News Books, Blackwell Scientific Publications Ltd., Oxford, UK. pp. 96–101.

Armstrong, J.D., Kemp, P.S., Kennedy, G.J.A., Ladle, M., and Milner, N.J. 2003. Habitat requirements of Atlantic salmon and brown trout in rivers and streams. Fish. Res. **62**: 143–170.

Baglinière, J.L., and Champigneulle, A. 1986. Population estimates of juvenile Atlantic salmon, *Salmo salar*, as indices of smolt production in the river Scorff, Brittany. J. Fish Biol. **29**: 467–482.

Baglinière, J.L., Maisse, G., and Nihouarn, A. 1993. Atlantic salmon (*Salmo salar*) wild smolt production. *In* Production of juvenile Atlantic salmon, *Salmo salar*, in natural waters. *Edited by* R.J. Gibson and R.E. Cutting. Can. Spec. Publ. Fish. Aquat. Sci. No. 118. pp. 189–201.

Baglinière, J.L., Marchand, F., and Vauclin, V. 2005. Interannual changes in recruitment of the Atlantic salmon (*Salmo salar*) population in the river Oir (Lower Normandy, France): relationships with spawner and in-stream habitat. ICES J. Mar. Sci. **62**: 695–707.

Bardonnet A., and Baglinière, J.L. 2000. Freshwater habitat of Atlantic salmon. Can. J. Fish. Aquat. Sci. **57**: 497–506.

Bernardo, J.M. 1979. Reference posterior distributions for Bayesian inference. J. R. Stat. Soc. Ser. B Stat. Methodol. **41**: 113–147 (with Discussion).

Bohlin, T., and Cowx, I.G. 1990. Implication of unequal probability of capture by electric fishing on the estimation of population size. *In* Development in electric fishing. *Edited by* I.G. Cowx. Fishing News Books, Blackwell Scientific Publications Ltd., Oxford, UK. pp. 145–155.

Bohlin, T., Hamrin, S., Heggberget, T.G., Rasmussen, G., and Svein, J.S. 1989. Electrofishing — theory and practice with special emphasis on salmonids. Hydrobiologia, **173**: 9–43.

Bohlin, T., Heggberget, T.G., and Strange, C. 1990. Electric fishing for sampling and stock assessment. *In* Fishing with electricity. *Edited by* I.G. Cowx and P. Lamarque. Fishing News Books, Blackwell Scientific Publications Ltd., Oxford, UK. pp. 112–139.

Brooks, S.P. 2003. Bayesian computation: a statistical revolution. Philos. Trans. R. Soc. Lond. A, **361**: 2681–2697.

Buckland, S.T. Newman, K.B., Thomas, L., and Koesters, N.B. 2004. State–space models for the dynamics of wild animal populations. Ecol. Model. **171**(1–2): 157–175.

Burnham, K.P., and Anderson, D.R. 2002. Model selection and multimodel inference: a practical information–theoretic approach. 2nd ed. Springer-Verlag, New York.

Carle, F.L., and Strub, M.R. 1978. A new method for estimating population size from removal data. Biometrics, **34**: 621–630.

Celeux, G., Forbes, F., Robert, C.P., and Titterington, D.M. 2006. Deviance information criteria for missing data. Bayesian Analysis, **1**(4): 651–674.

Clark, J.S. 2005. Why environmental scientists are becoming Bayesians. Ecol. Lett. **8**: 2–14.

Clark, J.S., and Bjørnstad, O.N. 2004. Population inference from messy data: errors, missing and hidden states, and lagged responses. Ecology, **85**: 3140–3150.

De Oliveira, E., Bez, N., and Prévost, E. 2001. Impact of local pollution on fish abundance using geostatistical simulations. *In* geoENV III — geostatistics for environmental applications. *Edited by* P. Monestiez, D. Allard, and R. Froidevaux. Kluwer Academic Publishers, Norwell, Massachusetts. pp. 181–191.

Dolan, C.R., and Miranda, L.E. 2003. Immobilization thresholds of electrofishing relative to fish size. Trans. Am. Fish. Soc. **132**: 969–976.

Dumas, J., and Prouzet, P. 2003. Variability of demographic parameters and population dynamics of Atlantic salmon (*Salmo salar* L.) in a southwest French river. ICES J. Mar. Sci. **60**: 356–370.

Elliott, J. 2001. The relative role of density in the stock–recruitment relationship of salmonids. *In* Stock, recruitment, and reference points. Assessment and management of Atlantic salmon. *Edited by* E. Prévost and G. Chaput. INRA Editions, Paris, France. pp. 25–55.

Fernandez, C., Ley, E., and Steel, M. 2002. Bayesian modelling of catch in a north-west Atlantic fishery. Appl. Stat. J. R. Stat. C, **51**(3): 257–280.

Gelman, A. 2006. Prior distributions for variance parameters in hierarchical models. Bayesian Analysis, **1**(3): 515–534.

Gelman, A., Carlin, J.B., Stern, H., and Rubin, D.B. 2004. Bayesian data analysis. 2nd ed. Col. Texts in Statistical Science, Chapman & Hall, New York.

Halley, J., and Inchausti, P. 2002. Lognormality of ecological time series. Oikos, **99**: 518–530.

Han, C., and Carlin, B.P. 2001. Markov chain Monte Carlo methods for computing Bayes factors: a comparative review. J. Am. Stat. Assoc. **96**: 1122–1132.

Hankin, D.G. 1984. Multistage sampling designs in fisheries research: applications in small streams. Can. J. Fish. Aquat. Sci. **41**: 1575–1591.

Harley, S.J., and Myers, R.A. 2001. Hierarchical Bayesian models of length-specific catchability of research trawl surveys. Can. J. Fish. Aquat. Sci. **58**: 1569–1584.

Harwood, J., and Stokes, K. 2003. Coping with uncertainty in ecological advice: lessons from fisheries. TREE, **18**(12): 617–622.

Hirst, D. 1994. An improved removal method for estimating animal abundance. Biometrics, **50**: 501–505.

Hoeting, J.A., Madigan, D., Raftery, A., and Volinsky, C. 1999. Bayesian model averaging: a tutorial. Stat. Sci. **4**(4): 382–417.

Kass, R.E., and Raftery, A.E. 1995. Bayes factors. J. Am. Stat. Assoc. **90**(430): 773–795.

Kennedy, G.J.A., and Crozier, W.W. 1995. Factors affecting recruitment success in salmonids. *In* The ecological basis for river management. *Edited by* D.M. Harper and A.J.D. Fergusson. Wiley & Sons, Chichester, UK. pp. 349–362.

King, R., and Brooks, S.P. 2001. On the Bayesian analysis of population size. Biometrika, **88**(2): 317–336.

Link, W.A., Cam, E., Nichols, J.D., and Cooch, E.G. 2002. Of bugs and birds: Markov chain Monte Carlo for hierarchical modeling in wildlife research. J. Wildl. Manag. **66**(2): 277–291.

Mäntyniemi, S., Romakkaniemi, A., and Arjas, E. 2005. Bayesian removal estimation of population size under unequal catchability. Can. J. Fish. Aquat. Sci. **62**: 291–300.

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Michielsen, C.G.J., and McAllister, M.K. 2004. A bayesian hierarchical analysis of stock–recruit data: quantifying structural parameter uncertainty. Can. J. Fish. Aquat. Sci. **61**: 1032–1047.

Milner, N.J., Elliott, J.M., Armstrong, J.D., Gardiner, R., Welton, J.S., and Ladle, M. 2003. The natural control of salmon and trout populations in streams. Fish. Res. **62**: 111–125.

Mitro, M.G., and Zale, A.V. 2000. Predicting fish abundance using single-pass removal sampling. Can. J. Fish. Aquat. Sci. **57**: 951–961.

Peterson, J.T., Thurow, R.F., and Gusevich, J.W. 2004. An evaluation of multipass electrofishing for estimating the abundance of stream dwelling salmonids. Trans. Am. Fish. Soc. **133**: 462–475.

Prévost, E., Parent, E., Crozier, W., Davidson, I., Dumas, J., Gudbergsson, G., Hindar, K., McGinnity, P., MacLean, J., and Sættem, L.M. 2003. Setting biological reference points for Atlantic salmon stocks. Transfer of information from data-rich to sparse-data situations by Bayesian hierarchical modelling. ICES J. Mar. Sci. **60**: 1177–1193.

Randall, R.G. 1990. Effect of water temperature, depth, conductivity and survey area on the catchability of juvenile Atlantic salmon by electric fishing in New Brunswick streams. *In* Developments in electric fishing. *Edited by* I.G. Cowx. Fishing News Books, Blackwell Scientific Publications Ltd., Oxford, UK. pp. 79–90.

Riley, S.C., Haedrich, R.L., and Gibson, R.J. 1993. Negative bias removal estimates of Atlantic salmon parr relative to stream size. J. Freshw. Ecol. **8**: 97–101.

Rivot, E., and Prévost, E. 2002. Hierarchical bayesian analysis of capture–mark–recapture data. Can. J. Fish. Aquat. Sci. **59**: 1768–1784.

Rivot, E., Prévost, E., Parent, E., and Baglinière, J.L. 2004. A Bayesian state–space modelling framework for fitting a salmon stage-structured population dynamic model to multiple time series of field data. Ecol. Model. **179**: 463–485.

Rosenberg, A.E., and Dunham, J.B. 2005. Validation of abundance estimates from mark–recapture and removal techniques for rainbow trout captured by electrofishing in small streams. N. Am. J. Fish. Manag. **25**: 1395–1410.

Schnute, J. 1983. A new approach to estimating populations by the removal method. Can. J. Fish. Aquat. Sci. **40**: 2153–2169.

Speas, D.W., Walters, C.J., Ward, D.L., and Rogers, R.S. 2004. Effects of intraspecific density and environmental variables on electrofishing catchability of brown and rainbow trout in the Colorado River. N. Am. J. Fish. Manag. **24**: 586–596.

Spiegelhalter, D.J., Thomas, A., and Best, N.G. 1996. Computation on graphical Bayesian models. *In* Bayesian statistics 5. *Edited by* J.M. Bernardo, J.O. Berger, A.P. Dawid, and A.F.M. Smith. Oxford University Press, Oxford, UK. pp. 407–425.

Spiegelhalter, D.J., Best, N.G., Carlin, B.P., and Van der Linde, A. 2002. Bayesian measures of model complexity and fit. J. R. Stat. Soc. B, **64**(3): 1–34.

Spiegelhalter, D.J., Thomas, A., and Best, N.G. 2003. WinBugs version 1.4. User Manual. MRC and Imperial College of Science, Technology and Medicine (available at: http://www.mrc-bsu.cam.ac.uk/bugs).

Wang, Y.-G., and Loneragan, N.R. 1996. An extravariation model for improving confidence intervals of population size estimates from removal data. Can. J. Fish. Aquat. Sci. **53**: 2533–2539.

Wikle, C.K. 2003. Hierarchical Bayesian models for predicting the spread of ecological processes. Ecology, **84**(6): 1382–1394.

Wyatt, R.J. 2002. Estimating riverine fish population size from single- and multiple-pass removal sampling using a hierarchical model. Can. J. Fish. Aquat. Sci. **59**: 695–706.

Wyatt, R.J. 2003. Mapping the abundance of riverine fish populations: integrating hierarchical Bayesian models with a geographic information system (GIS). Can. J. Fish. Aquat. Sci. **60**: 997–1006.

Appendix A. About the ignorability hypothesis of the missing data generating process

Following Gelman et al. (2004, p. 204), two conditions are sufficient to ensure ignorability: (*i*) data are missing at random (MAR); and (*ii*) parameters are distinct (DP). For the MAR condition to hold, the missing data mechanism can depend on the observed covariates and the data but it must be independent from the missing data values. The DP condition is verified when the parameters of the missing data process and the data generating process are a priori independent.

In our case study, we assumed that the missing data process is ignorable. To justify our view, it is useful to come back to the way in which the field operations are conducted and how the missing data process could be modelled accordingly. Having been frequently involved in the electrofishing operations, we contend that the field crew rely primarily on the available observations in hand, i.e., the number of fish caught at the first pass, to decide whether or not a second pass should be undertaken: the probability of missing data at the second pass is higher when the catch at the first pass is low. This may be modulated according to the year (for instance, see 1987 in Table 2), although it is difficult to retrospectively know which were the exact reasons leading the field crew to be less prone to undertake second passes in some years. The habitat type may influence the decision as well, e.g., it is possible that the field crew will be more willing to undertake a second pass in a riffle–rapid, the preferred habitat for juvenile salmon, than in a run. Based on this, a sensible modelling of the missing data process could be

$$(A1)\quad I(i,h,k) \sim \text{Bernoulli}(\xi(i,h,k))$$

$$\text{logit}(\xi(i,h,k)) = \varphi + \gamma \cdot C_1(i,h,k) + \eta_i + \lambda_h$$

where $I(i,h,k)$ is the indicator of missing data for the unit (i,h,k) as defined in the paper, $\xi(i,h,k)$ is the probability of missing data, $C_1(i,h,k)$ is capture at the first pass, and $\boldsymbol{\phi} = (\varphi, \gamma, \eta_i, \lambda_h)$ is the parameter vector of the missing data process, including year (η_i) and habitat type (λ_h) effects. In this model, the data "missingness" depends only on the observed data $C_1(i,h,k)$, the observed covariates (year and habitat), and the parameters of the missing data model $\boldsymbol{\phi}$. The data MAR condition is thus verified. There is no reason to hypothesize that the parameters $\boldsymbol{\phi}$ are not a priori independent from the parameters of the data-generating process, i.e., densities, capture probabilities, habitat and year effects on the densities and capture probabilities, and the associated hyperparameters (grand means and variances). We thus assumed by default that the DP condition holds as well.

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By looking at the observed data in Table 2, one may note that the decision to undertake a second pass (i.e., data missingness) shall not be (fully) independent of the density. However, this does not contradict the assumption of ignorability of the missing data mechanism by indicating that either the data MAR or the DP condition would be violated. In our case, it is just the consequence of the dependence of the missing data mechanism on the observed data C_1 as acknowledged in eq. A1.

Appendix B. Sensitivity analysis of model comparison criteria (BF and DIC) to alternative prior configurations

The influence of the prior on the BF may be high when using weakly informative priors as in the models described in the Material and methods section (Kass and Raftery 1995; Gelman et al. 2004). Marginal likelihoods P_M(DATA) and therefore BFs may also be sensitive to the choice of the system of constraints on the qualitative covariates effects (Fernandez et al. 2002). To assess these sensitivities, we fit and compared the four models $M_0,\ldots,M_3$ under several prior configurations denoted $PC_{i,j}$. The indices i and j denote the hyperparameter prior option and the alternative specifications of constraints, respectively, on the fixed effects of the habitat, $\beta_\phi(h)$s and $\beta_\pi(h)$s.

The baseline hyperparameter prior configuration, referred as $PC_{0,*}$, is the one described in the Material and methods section. It is based on vague prior distributions on all the hyperparameters of the model. In $PC_{1,*}$ we instead used the informative prior on the hyperparameters related to the catchability that might reflect expert knowledge (Table B1). Priors were set so that the marginal prior on π in each sampled unit is dome-shaped with a mode around 0.75 and small between-site and between-year variability. The priors on the hyperparameters for density remained unchanged compared with $PC_{0,*}$. In $PC_{2,*}$ informative hyperpriors were assigned to the hyperparameters related to catchability (the same as in $PC_{1,*}$) and density. For the later, priors were set to confine the between-year variability of the age-0+ density in a range that is compatible with the between-year variability of the smolt number estimated in the Oir River by Baglinière et al. (2005).

Table B1. Alternative hyperparameter prior configurations tested for the four competing models M_0 to M_3.

Prior configurations	Hyperparameters related to the probability of capture	Hyperparameters related to the density
$PC_{1,*}$	$\mu_\pi \sim$ Normal(1.5, $V_{\mu_\pi} = 0.1$)	Baseline $PC_{0,*}$
	$\sigma_\pi \sim$ Uniform on [0, $\sigma_{max} = 1$]	
	$\sigma_{\alpha_\pi} \sim$ Uniform on [0, $\sigma_{max} = 1$]	
	$V_{\beta_\pi} = 0.1$	
$PC_{2,*}$	$\mu_\pi \sim$ Normal(1.5, $V_{\mu_\pi} = 0.1$)	$\mu_\phi \sim$ Normal(0.5, $V_{\mu_\phi} = 0.02$)
	$\sigma_\pi \sim$ Uniform on [0, $\sigma_{max} = 1$]	$\sigma_\phi \sim$ Uniform on [0, $\sigma_{max} = 2$]
	$\sigma_{\alpha_\pi} \sim$ Uniform on [0, $\sigma_{max} = 1$]	$\sigma_{\alpha_\phi} \sim$ Uniform on [0, $\sigma_{max} = 3$]
	$V_{\beta_\pi} = 0.1$	$V_{\beta_\phi} = 0.02$

Note: The baseline configuration $PC_{0,*}$ is that described in the Materials and methods section.

The three prior configurations ($PC_{i,*}$, $i = 0,1,2$) were crossed with three alternative specifications of the constraints on the fixed effects of the habitat, $\beta_\phi(h)$s and $\beta_\pi(h)$s. $PC_{*,0}$ corresponds to the system of constraints described in the Material and methods section. The system of constraints in $PC_{*,1}$ is $\beta_\phi(h = 1) \sim$ Normal(0, V_{β_ϕ})$I(0,+\infty)$ and $\beta_\phi(h = 2) = 0$ and $\beta_\pi(h = 1) \sim$ Normal(0, V_{β_π}) and $\beta_\pi(h = 2) = 0$. The system of constraints in $PC_{*,2}$ is $\beta_\phi(h = 1) = 0$ and $\beta_\phi(h = 2) \sim$ Normal(0, V_{β_ϕ})$I(-\infty,0)$ and $\beta_\pi(h = 1) = 0$ and $\beta_\pi(h = 2) \sim$ Normal(0, V_{β_π}).

Results

The estimations of all unknown quantities are not sensitive to the choice of prior (results not shown). In terms of model comparison, the BF (Fig. B1) and DIC (Table B2) show some sensitivity to the prior configurations, but the main conclusions are unchanged. Indeed, apart from one case (BF with $PC_{1,2}$, where M_2 appears as a good candidate although M_0 remains preferred), both models M_2 and M_3 are always clearly discarded by BF. From the BF, the model M_0 is always the most credible, given the data for all prior configuration, and in most cases, M_0 clearly outcompetes the other models. According to the DIC, none of the four models can be clearly discarded because the differences between DIC values rarely exceed 5.

Table B2. Deviance information criterion (DIC) calculated for the four competing models M_0 to M_3 and under the nine prior configurations $PC_{0,0},\ldots,PC_{2,2}$ (see text and Table B1).

	Models			
Prior configurations	M_0	M_1	M_2	M_3
$PC_{0,0}$	815	817	814	814
$PC_{0,1}$	815	817	814	815
$PC_{0,2}$	815	817	814	814
$PC_{1,0}$	817	817	819	819
$PC_{1,1}$	826	826	830	832
$PC_{1,2}$	817	819	816	816
$PC_{2,0}$	822	823	830	830
$PC_{2,1}$	829	830	837	838
$PC_{2,2}$	822	824	833	834

The BFs of M_0 versus all other models computed from the harmonic mean of the likelihood values in eq. 9c show some instability (Fig. B1), which results from the occurrence of a

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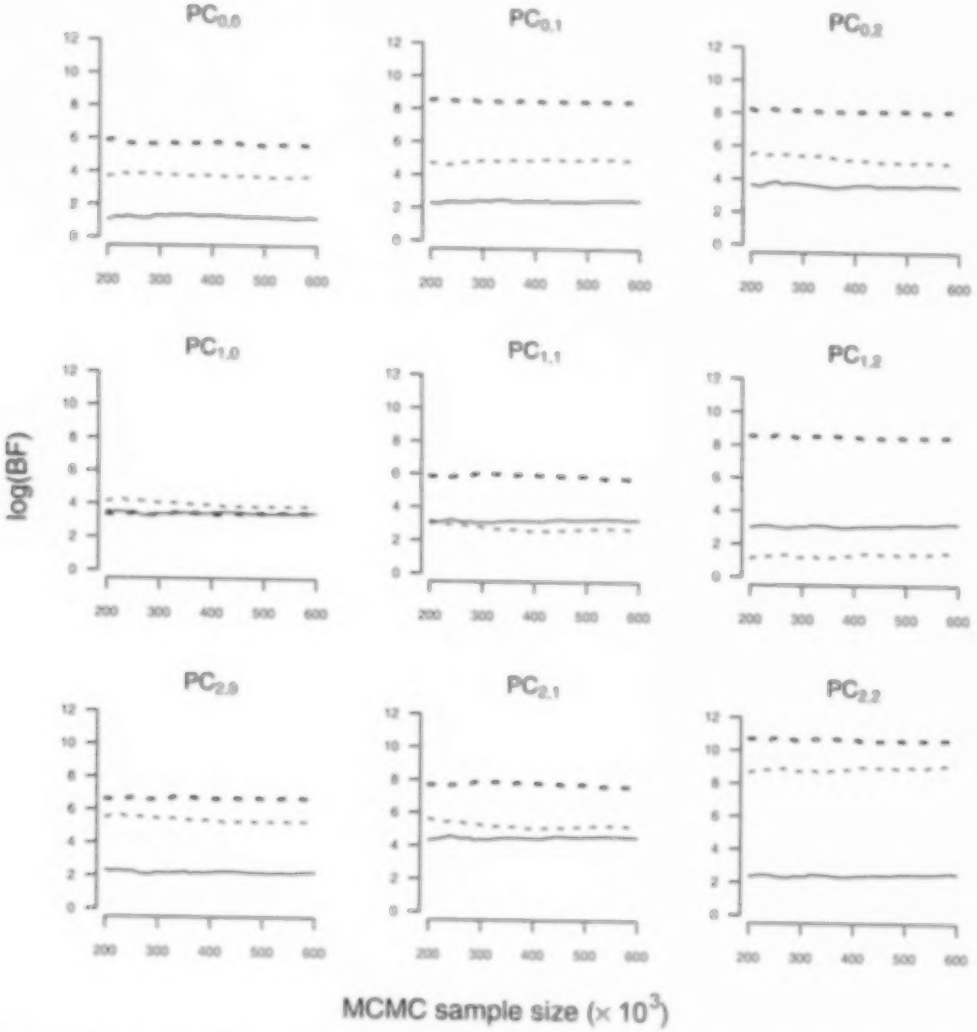
Fig. B1. Bayes factor (log scale) of the baseline model M_0 versus every other model calculated for the nine prior configurations $PC_{0,0}$,...,$PC_{2,2}$ (see text and Table B1). Solid line, M_0 vs. M_1; broken line, M_0 vs. M_2; dotted line, M_0 vs. M_3. Bayes factors are approximated from Markov chain Monte Carlo (MCMC) samples (size = 600 000) of deviance values according to eqs. 9*a*–9*c*. Eighty successive values of the Bayes factors are calculated by increasing the size of the MCMC sample from 200 000 to 600 000 with a step increment of 5000.



few very low values of the likelihood along the MCMC sampling that significantly influence the harmonic mean. However, in our case study, this instability is limited and never changes the results of the model comparison whatever the prior configuration used.

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with a detailed, point-by-point reply to all issues raised during the previous evaluation.

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General

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It has long been a policy of the *Canadian Journal of Fisheries and Aquatic Sciences* to not publish manuscripts that have been published elsewhere. The Editor considers a paper not eligible for publication if most of the content of the paper (*i*) is under consideration for publication or is published in a journal or book chapter; or (*ii*) is under consideration for publication or is published in a conference proceedings or a government publication, with a substantial circulation (distributed to 100 or more individuals over a wide area). Authors may place a draft of a submitted article on their Web site or their organization's server, provided that the draft is not amended once accepted for publication. We encourage authors to insert hyperlinks from preprints to the final published version on the NRC Research Press Web site (pubs.nrc-cnrc.gc.ca). Abstracts or extended abstracts related to conferences do not constitute prior publication. Extended abstracts are usually under 1000 words and do not include presentation of detailed tables and graphics of the results of the study. Further guidelines on extended abstracts are available from the Editorial Office's Web site (uoguelph.ca/~cjfas/).

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Authors may suggest names of referees that may or may not be used, but the selection of the referees is at the discretion of the Editor. When suggesting referees, please provide full addresses, telephone and fax numbers, and e-mail if available.

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Organize the manuscript on the basis of the purpose or scope of the study as stated in the Introduction. Ensure that the title and headings are in harmony with the statement of purpose.

Before writing any of the manuscript, list tentative headings in as few ranks as possible. Rework them until they appear to allow logical development for the reader; usually, chronological order is not effective. The findings will be more readily appreciated if methods, findings, and discussion are given in separate sections.

Organize tables and figures to facilitate comparisons, grouping related data in as few tables and figures as feasible. As far as possible, make the tables and figures clear without reference to the text.

Begin sections and paragraphs with topic sentences containing generalizations that lead readily to the particulars. Giving a conclusion first and then supporting it not only improves readability but also facilitates assessment by other scientists. Failure to give the most newsworthy generalizations first is one of the most prominent shortcomings in the presentation of manuscripts.

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Before writing any paragraphs, try writing the topic sentences for all of them and arranging these in appropriate order.

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The title page should contain the following. (*i*) The full title of the paper. (*ii*) Authors listed in the order in which they are to appear at the head of the printed article. (*iii*) Affiliation and address (including e-mail address) for each author. This should reflect the affiliation and address at the time of the study. Indicate current affiliations and addresses (including e-mail addresses) that differ from those in the by-line in a footnote. (*iv*) Name, address, telephone number, fax number, and e-mail address of the author responsible for correspondence.

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Like the title, the abstract enables readers to determine the paper's content and decide whether they need to read the entire paper. Begin the abstract with the main conclusion from the study and support it with the relevant findings. Limit details of methods to those needed in understanding what was done and work them into statements of findings. Avoid using phrases such as "... is discussed" or "... was found"; be specific. As the abstract is often divorced from the main body of the paper by abstracting and indexing services and is the only part of a paper some readers ever see, it is important that it accurately reflect the paper's contents and be completely self-contained (i.e., any *essential* references) in a retrievable form (e.g., R.B. Deriso. 1980. Can. J. Fish. Aquat. Sci. **37**: 268–282).

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Limit the Introduction largely to the scope, purpose, and rationale of the study. Restrict the literature review and other background information to that needed in defining the problem or setting the work in perspective. Try beginning with the purpose or scope of the work, defining the problem next, and

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adding guideposts to orient the reader. An introduction generally need not exceed 375–500 words.

Materials and methods

Materials and methods provides the framework for getting answers to the questions posed in the purpose of the work.

Limit the information on materials and methods to what is needed in judging whether the findings are valid. To facilitate assessment, give all the information in one section when possible. Refer to the literature concerning descriptions of equipment or techniques already published, detailing only adaptations. Often, it helps to begin statements on procedures with a phrase indicating the purpose, such as "To determine ... we ...". If the section is long, consider using subheadings corresponding to headings for the findings.

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Limit the Discussion to giving the main contributions of the study and interpreting particular findings, comparing them with those of other workers. Emphasis should be maintained on synthesis and interpretation and exposition of broadly applicable generalizations and principles. If these are exceptions or unsettled points, note them and show how the findings agree or contrast with previously published work. Limit speculation to what can be supported with reasonable evidence. End the Discussion with a short summary of the significance of the work and conclusions drawn. If the Discussion is brief and straightforward, it can be combined with the Results section.

Acknowledgements

Acknowledgements should be written in the third person. We strongly urge authors to limit acknowledgments to those who contributed substantially to scientific and technical aspects of the paper, gave financial support, or improved the quality of the presentation. Avoid acknowledging those whose contribution was clerical only.

Footnotes

Footnotes to material in the text should not be used unless they are unavoidable, but their use is encouraged in tables. Where used in the text, footnotes should be cited in the manuscript by superscript Arabic numbers (except in the tables, see below) and should be numbered serially beginning with any that appear on the title page. Each footnote should be typed on the manuscript page upon which the reference is made; **footnotes should not be included in the list of references.**

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The author is responsible for verifying each reference against the original article. Each reference must be cited in the text using the surnames of the authors and the year, for example, (Walpole 1985) or Green and Brown (1990). Depending on the sentence construction, the names may or may not be in parentheses, but the year always is. If there are three or more authors, the citation should give the name of the first author followed by et al. (e.g., Green et al. 1991). If references occur that are not uniquely identified by the authors' names and year, use *a*, *b*, *c*, etc., after the year, for example, Green 1983*a*, 1983*b*; Green and Brown 1988*a*, 1988*b*, for the text citation and in the reference list.

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References to unpublished data, manuscripts in preparation or submitted to other journals, progress reports, and unpublished papers given at annual meetings are not cited in the reference list but may be included in parentheses in the text, giving all authors' names and initials. For a private communication, year of communication should also be given (e.g., J.S. Jones (personal communication, 1999)). If consultants' reports or other documents of limited circulation must be cited, they should carry with them an availability statement explaining where the document can be obtained. If an unpublished book or article has been **accepted for publication**, include it in the reference list followed by the notation "In press". Do not include volume and page number in an in-press reference, as these are subject to change before publication.

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References should be selected judiciously and be largely restricted to significant, published literature. References should follow the form used in current issues of the Journal. The names of serials are abbreviated in the form given in *Chemical Abstracts Service Source Index* (*CASSI*) (Chemical Abstracts Service, 2540 Olentangy River Road, P.O. Box 3012, Columbus, OH 43210-0012, USA). In doubtful cases, authors should write the name of the serial in full. The Journal encourages the inclusion of issue numbers, which should be placed in parentheses after the volume number. The following bibliographic citations illustrate the punctuation, style, and abbreviations for references.

Examples of references types, including electronic references

Journal article with DOI:

Newbury, M.G., and Ashworth, A.C. 2004. A fossil record of colonization and response of lacustrine fish populations to climate change. Can. J. Fish. Aquat. Sci. **61**(10): 1807–1816. doi:10.1139/F04-113.

Journal article with URL:

Newbury, M.G., and Ashworth, A.C. 2004. A fossil record of colonization and response of lacustrine fish populations to climate change. Can. J. Fish. Aquat. Sci. **61**(10): 1807–1816. Available from pubs.nrc-cnrc.gc.ca/cgi-bin/rp/rp2_abst_e?cjfas_f04-113_61_ns_nf [accessed 28 October 2005].

Journal article available online only (with DOI):

van der Sanden, J.J., and Hoekman, D.H. 2005. Review of relationships between grey-tone co-occurrence, semivariance, and autocorrelation based image texture analysis approaches [online]. Can. J. Remote Sens. **31**(3): 207–213. doi:10.1139/rs03-011.

Entire issue of journal:

Gordon, D.C., Jr., and Hourston, A.S. (*Editors*). 1983. Proceedings of the Symposium on the Dynamics of Turbid Coastal Environments. Can. J. Fish. Aquat. Sci. **40**(Suppl. 1).

Report:

Sanders, W.W., Jr., and Elleby, H.A. 1970. Distribution of wheel loads in highway bridges. National Cooperative Highway Research Program Report 83, Transportation Research Board, National Research Council, Washington, D.C.

Book:

Williams, R.A. 1987. Communication systems analysis and design. Prentice-Hall, Inc., Englewood Cliffs, N.J.

Book in a series:

Scott, W.B., and Crossman, E.J. 1973. Freshwater fishes of Canada. Bull. Fish. Res. Board Can. No. 184.

Part of book:

Healey, M.C. 1980. The ecology of juvenile salmon in Georgia Strait, British Columbia. *In* Salmonid ecosystems of the North Pacific. *Edited by* W.J. McNeil and D.C. Himsworth. Oregon State University Press, Corvallis, Oreg. pp. 203–229.

Paper in conference proceedings:

Kemp, A.L.W. 1969. Organic matter in the sediments of Lakes Ontario and Erie. *In* Proceedings of the 12th Conference on Great Lakes Research, Ann Arbor, Mich., 5–7 May 1969. International Association for Great Lakes Research, Ann Arbor, Mich. pp. 237–249.

Institutional publications and pamphlets:

Dzikowski, P.A., Kirby, G., Read, G., and Richards, W.G. 1984. The climate for agriculture in Atlantic Canada. Available from the Atlantic Advisory Committee on Agrometeorology, Halifax, N.S. Publ. ACA 84-2-500. Agdex No. 070.

Corporate author:

American Public Health Association, American Water Works Association, and Water Pollution Control Federation. 1975. Standard methods for the examination of water and wastewater. 14th ed. American Public Health Association, American Water Works Association, and Water Pollution Control Federation, Washington, D.C.

Thesis:

Keller, C.P. 1987. The role of polysaccharidases in acid wall loosening of epidermal tissue from young *Phaseolus vulgaris* L. hypocotyls. M.Sc. thesis, Department of Botany, The University of British Columbia, Vancouver, B.C.

Web site citation:

Quinion, M.B. 1996. Citing online sources: advice on online citation formats [online]. Available from worldwidewords.org/articles/citation.htm [accessed 20 October 2005].

Translation:

Koike, A., and Ogura, B. 1977. Selectivity of meshes and entrances of shrimp traps and crab traps. J. Tokyo Univ. Fish. **64**: 1–11. [Translated from Japanese by Can. Transl. Fish. Aquat. Sci. 4950, 1983.]

Tables

Tables must be typed on separate pages, placed after the list of references, and numbered with Arabic numerals in the order cited in the text. The title of the table should be a concise description of the content, no longer than one sentence, that allows the table to be understood without detailed reference to the text. Column headings should be brief, but may be amplified by footnotes. Vertical rules should not be used. A copy of the Journal should be consulted to see how tables are set up and where the lines in them are placed. Footnotes in tables should be designated by symbols (in the order *, †, ‡, §, ||, ¶, #) or superscript lowercase italic letters. Descriptive material not designated by a footnote may be placed under a table as a **Note**. Numerous small tables should be avoided, and the number of tables should be kept to a minimum.

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Supplementary material

Supplementary material (or data) consists of extra tables, figures (maps), detailed calculations, and data sets produced by the authors as part of their research, but not essential for understanding or evaluating the paper, and not published with the article in the print edition of the Journal. Depending on the policy of the Journal, such material may or may not be peer reviewed with the article. Supplementary material should be submitted with the article. During Web submission (**OSPREY**), relevant files should be attached under "Supplementary data". The National Research Council of Canada maintains a depository in which supplementary material may be placed, either at the request of the author or at the suggestion of the Editor. In addition, supplementary material can be made available at no charge in its native file format on the Journal Web site. It will be linked from the Web page of the associated article. Tables and figures should be numbered in sequence separate from those published with the paper (e.g., Fig. S1, Table S1). The supplementary material should be referred to in the printed article by footnotes. Printed copies of material in the depository may be purchased from the Depository of Unpublished Data, CISTI, National Research Council of Canada, Ottawa, ON K1A 0R6, Canada.

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Maps must have very **clear, bold patterns** and must show longitudes and latitudes (or UTM coordinates) and a scale to ensure proper identification of study locations. On **maps of Quebec**, the official name of municipalities must be used (e.g., Québec, Montréal, Clarke City) and physical features must be in French (e.g., Lac Bienville) except for those that are considered of pan-Canadian significance. Areas of pan-Canadian significance have an official form in English and French (e.g., Atlantic Ocean and Océan Atlantique) and should appear in the language of the paper. Quebec (the province) must also appear in the language of the paper. For a complete list of names of areas of pan-Canadian significance, see pp. 236–237 of *Le guide du rédacteur* (2nd ed., 1996), published by Public Works and Government Services Canada, Ottawa, ON K1A 0S5.

Photographs

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Colour illustrations will be at the author's expense. Further details on prices are available from Cecily Pearson, Managing Editor of the Journal (613-993-9099; fax: 613-952-7656; e-mail: cecily.pearson@nrc-cnrc.gc.ca).

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Multimedia formats — Audio and video clips in the major multimedia formats are now accepted for NRC Research Press journals published in full-text HTML. For accepted formats, see the Electronic graphic list published on the Journal Web site.

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As a general guide for biological terms, *The CSE Manual for Authors, Editors, and Publishers: Scientific Style and Format* (7th ed., 2006) published by the Council of Science Editors, Reston, VA 20190, USA, is recommended.

Spelling

Spelling should follow *Webster's Third New International Dictionary* or the *Oxford English Dictionary*. Authors are responsible for consistency in spelling.

Nomenclature, abbreviations, and acronyms

Nomenclature and abbreviations should follow the rules recommended by the International Union of Biochemistry (IUB) Committee of Editors of Biochemical Journals with support of IUPAC. As a general guide for biological terms, *The CSE Manual for Authors, Editors, and Publishers: Scientific Style Format* (7th ed., 2006), published by the Council of Biology Editors, Reston, VA 20190, USA, is recommended. For enzyme nomenclature, *Enzyme Nomenclature (1992): Recommendations of the Nomenclature Committee of the International Union of Biochemistry and Molecular Biology* (Academic Press, San Diego, Calif.) should be followed.

Abbreviations and acronyms that are standard in the discipline need not be defined. All others must be defined when they are first mentioned in the text and those with more than one meaning should be avoided.

Units of measurement

SI units (Système international d'unités) should be used or SI equivalents should be given. Avoid ambiguous forms such as g C/m^2/day; use g C·m^{-2}·day^{-1}. This system is explained and other useful information is given in the *Metric Practice Guide* (2000) published by CSA International (178 Rexdale Blvd., Toronto, ON M9W 1R3, Canada). For practical reasons, some exceptions to SI units are allowed. Units such as kilocalorie, reciprocal centimetre (wave number), and atmosphere may be used for the foreseeable future.

Statistical analyses

The assumptions and (or) the model underlying any statistical analysis should be clearly stated. Symbols such as * and **, denoting levels of significance, should not be used except in conjunction with the actual values of the associated test statistic; actual *p* values are preferred.

Fish

The Journal follows the names and spelling for fishes recommended in *Common and Scientific Names of Fishes from the United States, Canada, and Mexico* (6th ed., Spec. Publ. No. 29, American Fisheries Society, 2004) and the gene nomenclature for protein-coding loci outlined in Shaklee et al. (Trans. Am. Fish. Soc. **119**: 2–15, 1990).

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In writing long numbers, the digits should be separated into groups of three, counted from the decimal marker to the left and right. The separator should be a space and not a comma, period, or any other mark, for example, 25 562 987 and not 25,562,987. In English text, the decimal marker should be a point, for example, 0.1 mL and not 0,1 mL. The decimal point in all numbers between 1 and –1, except 0, must be preceded by a 0. The sign × should be used to indicate multiplication, e.g., 3×10^5 and not $3 \cdot 10^5$.

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Journal canadien des sciences halieutiques et aquatiques

Orientation du Journal et directives de soumission de manuscrits

La Rédaction encourage la soumission d'articles contribuant à l'enrichissement des connaissances des sciences halieutiques et aquatiques. Les articles peuvent porter sur les cellules, les organismes, les populations, les communautés, les écosystèmes ou les procédés qui affectent les systèmes aquatiques. Ils peuvent traiter de disciplines variées y compris la biologie et l'écologie des organismes d'eau douce et d'eau salée, la limnologie, l'océanographie, la physiologie, la toxicologie, la génétique, l'économie, les maladies et la gestion. Les articles sont choisis selon la portée et l'importance des nouvelles connaissances ou idées qu'ils contiennent. On accorde la préséance aux articles qui contribuent à la compréhension de phénomènes observés et à l'interprétation de résultats expérimentaux.

Nous invitons les auteurs à soumettre des articles ayant des objectifs précis ou relevant des hypothèses, concepts ou questions vérifiables et se terminant par de solides conclusions ou d'utiles synthèses. Ces articles enrichissent, changent, mettent en question ou réorientent les connaissances acquises sur divers aspects des sciences aquatiques. **La raison d'être de l'analyse et l'interprétation des résultats doivent être situées dans un vaste contexte disciplinaire ou interdisciplinaire.** Les articles de méthodologie et de modélisation doivent inclure des applications et prouver la supériorité de la méthodologie ou du modèle explicité.

La Rédaction décourage la soumission d'articles simplement descriptifs (à moins qu'il ne s'agisse de nouvelles disciplines), d'application très limitée (applicable à une seule année, une seule région ou un seul taxon, portant sur un unique composé chimique, etc.); d'articles qui ne font que reprendre les principes énoncés dans des articles précédents; ou d'articles rendant compte de l'application de normes sans gain de méthodologie. Les études préliminaires ou fragmentaires, ou dont la pertinence à grande échelle n'est pas démontrée, et les interprétations purement spéculatives sont carrément rejetées.

Les articles doivent être aussi complets que possible. S'il est impossible d'inclure toute les données pertinentes dans un seul article, l'auteur devra inclure des renvois à des articles connexes et soumettre ceux-ci avec son propre article.

Types de manuscrits

Le Journal publie le genre de textes suivants :

Articles — Études de vaste portée qui constituent de nouvelles contributions à la science.

Perspectives — Synthèses, synthèses critiques ou réévaluations de concepts ou de paradigmes couramment admis.

Discussions — Commentaire ou réplique sur des sujets récemment abordés dans le Journal.

Communications rapides — Présentations de nouveaux concepts, descriptions de nouvelles méthodologies ou courts textes sur des sujets d'actualité ou controversés.

On peut obtenir les caractéristiques précises de chacun de ces genres sur le site Web du Bureau de la rédaction (uoguelph.ca/~cjfas/).

Langue

Les manuscrits doivent être rédigés de manière claire et concise, **en français ou en anglais correct**. Les auteurs pour qui le français ou l'anglais est une langue seconde devraient faire réviser leur manuscrit par une personne dont la langue maternelle est celle du texte avant de soumettre leur manuscrit. Un style de qualité accélère et facilite l'examen et la publication des manuscrits.

Un résumé rédigé dans la langue du manuscrit doit accompagner chaque soumission. Les résumés sont traduits en anglais ou en français, selon le cas, par le traducteur du Journal. En revanche, les auteurs qui peuvent soumettre leur résumé en français et en anglais sont invités à le faire.

Frais d'impression par page

Il n'y a pas de frais d'impression par page dans le *Journal canadien des sciences halieutiques et aquatiques.*

Objectif des recommandations

Pour **faciliter la publication**, les auteurs doivent vérifier l'exactitude, l'uniformité et la lisibilité des symboles, des abréviations et des termes techniques. Les Presses scientifiques du CNRC se réservent le droit d'assurer la qualité technique du Journal. Les auteurs voudront consulter un récent numéro du Journal pour s'enquérir des exigences en matière de présentation, en particulier à l'égard des tableaux et de la bibliographie. **La non-conformité des manuscrits et des illustrations aux exigences décrites ci-dessous risque de retarder la publication.**

Soumission

Nouveaux manuscrits

Les auteurs peuvent soumettre leur manuscrit par le Web ou par courriel (cjfas@utoronto.ca). On encourage la soumission Web par **OSPR**EY (système de soumission et d'examen en direct des articles).

Par le Web

Les auteurs peuvent soumettre leur manuscrit par **OSPR**EY, le système de soumission et d'examen en direct des articles (pubs.nrc-cnrc.gc.ca/jcsha/osprey). **OSPR**EY est optimisé pour les fureteurs Netscape 7.0 et Internet Explorer 6.0 (ou toute version ultérieure). Au moment de l'inscription, les auteurs seront invités à choisir un nom d'utilisateur et un mot de passe. L'accès aux manuscrits est protégé par le système

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de nom d'utilisateur et de mot de passe. Les auteurs peuvent s'inscrire sur le site à tout moment; une seule inscription est nécessaire. Le profil des auteurs et des examinateurs ayant déjà utilisé le système **OSPR**EY du Journal par le passé demeure actif. Pour accéder au système, il suffit alors d'entrer son adresse de courriel dans le champ « Mot de passe oublié » du site Web.

Les auteurs qui ont besoin d'une aide technique quant au processus de soumission sur le Web peuvent communiquer avec Louis Lafleur au 613-998-9432 ou par courriel à louis.lafleur@nrc-cnrc.gc.ca, de 8 h 00 à 16 h 00 (HNE).

Un guide de l'utilisateur détaillé est offert sur le site Web.

Les auteurs doivent accompagner leur manuscrit d'une lettre de présentation. Les tableaux et les illustrations peuvent soit faire partie du fichier de manuscrit ou être téléchargés individuellement vers le serveur. **OSPR**EY accepte la plupart des fichiers de format texte et graphique. (c.-à-d., .cdr, .doc, .eps, .jpg, .gif, .pdf, .ppt, .ps, .psd, .tif, .wpd et .xls)

Actuellement, les Presses scientifiques du CNRC n'acceptent pas les documents Word de la version 12 de Microsoft Office (extension .docx). Veuillez noter que le fait de sauvegarder des documents .docx dans un autre format (tel que .doc, .rft ou .txt) pourrait avoir des répercussions sur le formatage ou entraîner une perte de données. Ainsi, nous demandons aux auteurs, qui convertissent leur manuscrit de format .docx à un autre, de le vérifier attentivement avant de le soumettre à des fins d'examen, et ce, pour éviter toute erreur ou perte de données éventuelle.

Lors de la première soumission d'un manuscrit à un examen par les pairs, une version à faible résolution des illustrations devrait être téléchargée afin de limiter la taille des fichiers. La soumission des manuscrits devrait se faire l'ordinateur qui contient tous les fichiers pertinents. Le processus de soumission de manuscrit exige environ 10 minutes, mais le temps de téléchargement vers le serveur variera en fonction du type de connexion Internet utilisé.

Toute correspondance relative au manuscrit soumis par **OSPR**EY sera envoyée à la personne identifiée comme auteur correspondant au moment de la soumission du manuscrit. De plus, toute correspondance se fera par voie de courriel.

Manuscrits révisés

Quant aux révisions, l'auteur correspondant sera avisé par courriel d'une demande de révision.

Manuscrits acceptés

L'auteur sera avisé que son manuscrit a été accepté. On lui demandera alors de soumettre la version définitive du manuscrit et tous les fichiers connexes, y compris les tableaux, les illustrations et les données supplémentaires par **OSPR**EY ou par courriel. (Reportez-vous au site Web de la revue pour consulter la liste complète des formats des manuscrits acceptés.)

Le **texte** (y compris les tableaux) doit être soumis en format de traitement de texte (de préférence WordPerfect, Microsoft Word ou TeX, en version Windows ou Macintosh). Des macros TeX pour la préparation des manuscrits acceptés sont disponibles en direct à ftp.tex.ac.uk/tex-archive/macros/latex/contrib/nrc/, ftp.dante.de/tex-archive/macros/latex/contrib/nrc/ et ctan.tug.org/tex-archive/macros/latex/contrib/nrc/.

Lors de la soumission de la version définitive du manuscrit, pour assurer la qualité optimale de reproduction et d'impression des illustrations, les auteurs doivent :

(i) Télécharger les fichiers d'illustrations séparément du manuscrit.

(ii) S'assurer que la résolution des fichiers d'illustrations est élevée.

(iii) S'assurer que les illustrations sont dans leur format original (p. ex. PhotoShop, Adobe Illustrator, Excel, CorelDraw, SigmaPlot), et non intégrées à un document Word ou converties dans un autre format. Toutefois, si les illustrations sont dans un format que les Presses scientifiques du CNRC n'acceptent pas, les auteurs peuvent fournir les illustrations dans des fichiers PostScript ou PDF de haute qualité et à haute résolution. Il est aussi possible d'envoyer une illustration en différents formats; l'éditeur choisira le format qui donne les meilleurs résultats.

(iv) S'assurer de télécharger la bonne version et la version plus récente des fichiers.

Renseignements complémentaires sur la soumission

Lettre de présentation

L'auteur correspondant doit accompagner son manuscrit d'une lettre de présentation qui fait état :

(i) des principaux points et de l'importance du travail;

(ii) de la participation de tous les auteurs au manuscrit et de leur approbation de ce dernier;

(iii) de l'assurance que le manuscrit en question n'est pas en cours d'examen aux fins de publication dans une autre revue;

(iv) de suggestions quant aux arbitres éventuels;

(v) d'autres manuscrits, y compris de résumés détaillés, contenant une information identique ou similaire à celle contenue dans le manuscrit soumis;

(vi) des numéros de téléphone et de télécopieur ainsi que du courriel et de l'adresse de chaque auteur;

(vii) de tout conflit d'intérêts, réel ou perçu (cf. « Conflit d'intérêts et divulgation » sous la rubrique « Éthique »).

Cession ou licence de droits d'auteur

Si le directeur scientifique accepte d'examiner un manuscrit à des fins de publication, le Bureau de la rédaction demandera aux auteurs de lui retourner dans les plus brefs délais les licences ou les formulaires de cession de droits d'auteur dûment signés. Pour que la publication d'un manuscrit soit autorisée, tous les auteurs doivent au préalable remplir un formulaire ou une licence qui cède leurs droits d'auteur au CNRC ou autorise le CNRC à publier leur document. La plupart des auteurs doivent signer le formulaire de cession de droits d'auteur, qui transfère tous les droits au CNRC. Les fonctionnaires des pays du Commonwealth doivent signer une licence qui leur permet de conserver les droits de la Couronne. Pour leur part, les fonctionnaires des États-Unis doivent signer une entente de publication, puisque leurs documents sont exclus de la protection des droits d'auteur des États-Unis. Les auteurs peuvent obtenir ces formulaires auprès du directeur scientifique, dans le premier numéro d'un volume ou dans le site Web du Journal (pubs.nrc-cnrc.gc.ca/fra/formulaires/index.html).

Processus de révision

Réception des manuscrits

Lorsque le directeur scientifique acceptera de prendre en considération un manuscrit à des fins de publication, l'auteur

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correspondant recevra un accusé de réception officiel, et le Bureau de la rédaction lui demandera de remplir les formulaires nécessaires dans les plus brefs délais. Dans l'éventualité où un manuscrit soumis ne serait pas retenu pour examen en vue de publication, l'auteur correspondant serait avisé de cette décision par courriel.

La conformité du manuscrit aux *Recommandations aux auteurs* sera vérifiée par un lecteur technique. Les manuscrits non conformes ainsi que ceux qui ne réussissent pas à définir clairement l'objet de la recherche pourront être renvoyés à l'auteur correspondant pour que la présentation soit corrigée avant que le contenu n'en soit examiné.

Examen par les pairs/évaluation

Chaque article est habituellement soumis à une évaluation par deux réviseurs. Toutefois, le directeur scientifique renverra sans les évaluer tout article qui ne reflète pas la portée ou le caractère du Journal et les articles qui débordent des limites imposées pour la publication sous forme de « résumés approfondis ». On obtiendra les directives à cet égard sur le site Web du Bureau de la rédaction à uoguelph.ca/~cjfas/. Les articles soumis aux fins de publication dans un supplément sont soumis au même rigoureux exercice d'examen que les articles des numéros réguliers.

On demande habituellement aux auteurs d'examiner les commentaires des réviseurs et de modifier leur texte en conséquence en 60 jours, tout au plus. Faute de respecter ce délai, l'article renvoyé par l'auteur sera traité comme une nouvelle soumission à moins que l'auteur n'ait au préalable dûment communiqué avec le Bureau de la rédaction.

Manuscrits resoumis

Les auteurs qui soumettent un manuscrit précédemment refusé ou retiré doivent indiquer dans leur lettre de présentation le numéro de manuscrit de leur première soumission. Les manuscrits ainsi resoumis sont traités comme de nouveaux manuscrits. Les auteurs peuvent soumettre le nouveau manuscrit par courriel ou par **OSPR**EY, accompagné d'une réponse détaillée et systématique à toutes les questions soulevées au cours de l'évaluation précédente.

Processus de publication

Généralités

La Rédaction vérifie tous les articles soumis afin de s'assurer qu'ils respectent les *Recommandations aux auteurs* et qu'ils sont accompagnés de toute la documentation d'appui nécessaire. Tout élément posant problème sera examiné par la Rédaction en consultation avec l'auteur correspondant. Une fois que tous les problèmes sont résolus par la Rédaction et que tous les formulaires de cession des droits d'auteur dûment signés par les auteurs sont reçus, le manuscrit est acheminé aux Presses scientifiques du CNRC, à Ottawa, en vue de sa publication. La préparation finale des manuscrits est assurée par un lecteur-rédacteur responsable de l'uniformité de la présentation et du style.

Correspondance avec les Presses scientifiques du CNRC

Après qu'un article a été accepté, toute correspondance doit être adressée aux Presses scientifiques du CNRC, Conseil national de recherches du Canada, Ottawa, ON K1A 0R6, Canada (télécopieur : 613-952-7656; courriel : pubs@nrc-cnrc.gc.ca; URL : pubs.nrc-cnrc.gc.ca). Les Presses scientifiques du CNRC se réservent le droit d'apporter des modifications rédactionnelles mais ne modifieront pas la substance d'un article sans préalablement consulter l'auteur et la directrice scientifique principale.

Épreuves

Une épreuve renfermant les illustrations, le manuscrit annoté, et un bon de commande de tirés à part seront envoyés à l'auteur correspondant. **Les épreuves doivent être relues attentivement car elles ne seront pas revues par les Presses scientifiques du CNRC.** Elles doivent en outre être renvoyées dans les 48 heures suivant leur réception. Au stade des épreuves, il n'est plus temps d'apporter des modifications importantes ni de faire des ajouts ou des suppressions. Les frais occasionnés par des modifications excessives devront être assumés par les auteurs.

Tirés à part

Pour obtenir des tirés à part, il convient de remplir le bon de commande à cet effet, d'y annexer le paiement pertinent (chèque, numéro de carte de crédit, numéro de bon d'achat ou pièce de journal interne) et de renvoyer le tout en même temps que les épreuves et l'article corrigés. Le tarif des tirés à part commandés après la publication est fortement majoré. **Le Journal n'offre pas de tirés à part gratuits. Les tirés à part commandés ne sont postés qu'après réception d'un numéro du bon d'achat ou du paiement pertinent.**

Permission de reproduction de documents protégés par droits d'auteur

Les auteurs d'un manuscrit qui contient de la documentation déjà publiée (tableaux, illustrations, schémas, etc.), et donc assujettie aux droits d'auteur, doivent obtenir **une permission écrite, de la part du titulaire de ces droits d'auteur**, de reproduire l'information en question **en format imprimé et électronique**. Les permissions écrites doivent accompagner le manuscrit soumis, sans quoi le processus de publication pourra être retardé. Cette lettre sera exigée avec toute mention du type « tirée de... ». Si une illustration est modifiée, de sorte qu'une telle autorisation n'est pas requise, la formulation doit être explicit : « modifiée d'après... ». Si l'illustration est reconstituée à partir d'informations tirées d'autres auteurs la mention doit être du même type que pour une référence.

Permission de republication de documentation publiée dans les revues des Presses scientifiques du CNRC

Toute demande de permission de reproduction ou de republication partielle ou intégrale d'un manuscrit doit être adressée à Roxanne Landriault, des Presses scientifiques du CNRC (613-990-2254; télécopieur : 613-952-7656; courriel : roxanne.landriault@nrc-cnrc.gc.ca).

Éthique

Généralités

Les normes d'éthique auxquelles doivent se conformer les auteurs, les examinateurs et les directeurs scientifiques sont décrites dans la Politique éditoriale des Presses scientifiques du CNRC (publiée dans le numéro de janvier 1996 du *Journal*

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canadien des sciences halieutiques et aquatiques, diffusée sur le site Web du Journal à pubs.nrc-cnrc.gc.ca/fra/politique/index.html ou disponible auprès des Presses scientifiques du CNRC).

Reproduction et rediffusion

En vertu d'une politique de longue date, le *Journal canadien des sciences halieutiques et aquatiques* refuse de publier des articles qui ont été publiés ailleurs. Le directeur scientifique juge un manuscrit inadmissible si le manuscrit en question (*i*) est en cours d'examen en vue d'être publié ou a déjà été publié dans un périodique ou dans un livre, ou (*ii*) est en cours d'examen en vue d'être publié ou a déjà été publié dans un compte rendu de conférence ou dans une publication officielle ouvertement distribuée à plus de 100 exemplaires. Les auteurs peuvent proposer, sur leur site Web ou sur le serveur de leur institution, une ébauche d'un article soumis, à condition que l'ébauche ne soit aucunement modifiée après l'acceptation du manuscrit. Les auteurs sont invités à inclure, sur la version préimprimée de leur manuscrit, un lien hypertexte vers sa version définitive sur le site Web des Presses scientifiques du CNRC (pubs.nrc-cnrc.gc.ca). Les résumés concis ou détaillés inclus dans les comptes rendus de conférences ne constituent pas une « publication antérieure ». Un « résumé détaillé » est un document de 1000 mots ou moins qui ne comprend ni tableaux détaillés ni illustrations des résultats de l'étude. Des renseignements supplémentaires sur les résumés détaillés sont disponibles sur le site Web du Bureau de la rédaction (uoguelph.ca/~cjfas/).

Déclaration de la paternité du manuscrit

Dans sa lettre de présentation, l'auteur correspondant doit garantir que les auteurs ont tous contribué de près au manuscrit et ont approuvé la version soumise.

Suggestion d'examinateurs

Les auteurs peuvent suggérer des examinateurs. Ils doivent fournir l'adresse complète, les numéros de téléphone et de télécopieur, ainsi que l'adresse de courriel (dans la mesure du possible) de ces personnes. Le directeur scientifique n'est aucunement tenu de se limiter à ces suggestions.

Conflit d'intérêts et divulgation

Le directeur scientifique reconnaît la possibilité que des conflits d'intérêts réels ou perçus surviennent à la suite de circonstances intellectuelles, personnelles ou financières liées aux travaux de recherche. Les manuscrits doivent inclure une divulgation de toute source de financement de la recherche. De plus, la lettre de présentation doit expliquer tout conflit d'intérêts, réel ou perçu, qui pourrait survenir lors du processus d'examen par les pairs. Si de tels conflits ne sont pas divulgués, le manuscrit pourrait être refusé.

Photos de personnes

La publication d'une photo qui montre une personne identifiable exige que la personne concernée signe une lettre ou un formulaire qui autorise les Presses scientifiques du CNRC à publier cette photo.

Retouche photographique

Le Journal estime que les photographies numériques font partie des données. Aussi est-il impératif que les images numériques soumises reproduisent fidèlement l'image d'origine. Toute retouche à l'aide d'un logiciel graphique doit être explicitée dans les méthodes, notamment quant au logiciel utilisé et aux techniques appliquées pour améliorer ou modifier l'illustration. Une telle explication assure la constance des méthodes et l'intégrité scientifique des travaux. La suppression des artéfacts ou de toute donnée non essentielle contenue dans l'image est découragée.

Sections du manuscrit

Disposition et organisation

Le manuscrit, y compris la bibliographie, les tableaux et les légendes d'illustrations, doit être composé à **double interligne** sur des feuilles de papier de 21,5 sur 28 cm (8,5 po sur 11 po) ou ISO A4. Chaque page doit être numérotée, en commençant par la page de titre. Les lignes du texte doivent aussi être numérotées. Le texte destiné à être publié en italique doit être présenté en italique, non pas souligné. Les auteurs utiliseront des caractères en majuscule seulement lorsque cela s'avérera pertinent.

Les auteurs devraient structurer le manuscrit en fonction de l'énoncé des objectifs ou de la portée de l'étude présentée dans l'introduction. Il est particulièrement important que le titre et les en-têtes reflètent l'énoncé des objectifs.

Avant de commencer la rédaction du manuscrit, les auteurs devraient dresser une liste provisoire des en-têtes, avec le moins de subdivisions possible, et remanier cette liste jusqu'à ce qu'elle reflète une démarche logique, intelligible pour le lecteur. Habituellement, l'ordre chronologique ne sera pas satisfaisant. En effet, il sera plus facile de suivre le texte si les méthodes, les résultats et la discussion font partie de sections distinctes.

Les auteurs devraient organiser les tableaux et les illustrations de manière à faciliter les comparaisons et regrouper les données apparentées de façon à réduire au minimum le nombre de tableaux et d'illustrations. Dans la mesure du possible, les tableaux et les figures devraient être suffisamment explicites pour que le lecteur n'ait pas à se reporter au texte.

Les auteurs devraient commencer les sections et les paragraphes par des énoncés généraux qui aboutissent naturellement à des énoncés pointus. La présentation de la conclusion dans un premier temps et de sa justification dans un deuxième facilite considérablement la lecture et l'évaluation par les scientifiques. Lors de la rédaction des manuscrits, le défaut le plus courant consiste à omettre de présenter dès le début du texte les généralités les plus dignes de mention.

Les auteurs doivent veiller à ce que le contenu de chaque section soit pertinent à l'en-tête et que le contenu de chaque paragraphe se rapporte à la première phrase du paragraphe (la « phrase d'ouverture »).

Avant de rédiger les paragraphes, les auteurs devraient composer la phrase d'ouverture de chaque paragraphe et disposer chacune de celles-ci dans l'ordre approprié.

Titre

Les auteurs doivent limiter le titre à ce que démontre le manuscrit. Le titre est un élément fondamental de l'article et doit refléter clairement et brièvement le contenu du manuscrit. Le titre a deux fonctions : (*i*) il permet au lecteur de juger si, oui ou non, l'article est susceptible de l'intéresser et (*ii*) il devrait fournir suffisamment d'information pour permettre au lecteur de juger de la portée et de l'importance potentielle du

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contenu. Les mots du titre devraient fournir un maximum d'information et identifier la nature de la recherche, de l'organisme utilisé et, le cas échéant, la démarche technique (p. ex. radiographie, chromatographie, analyse mathématique). Les titres ne devraient pas commencer par un chiffre ou par des prépositions d'introduction telles que « Sur » ou « Vers », ou des expressions telles que « Contribution à ... » ou « Recherche sur ... ». Des titres judicieux facilitent considérablement le classement des publications et leur utilisation par les scientifiques et les bibliothécaires et de même que leur dépouillement par les indexateurs. Les titres en série devraient être évités.

Page de titre

La page de titre doit comprendre les suivants. (*i*) Le titre intégral du manuscrit. (*ii*) Le nom des auteurs, dans l'ordre dans lequel ces noms doivent apparaître dans l'intitulé de l'article imprimé. (*iii*) L'affiliation et l'adresse (y compris l'adresse de courriel) de chaque auteur pendant les recherches. Les changements d'affiliations et d'adresses (y compris d'adresse de courriel) devront être indiqués en note infrapaginale. (*iv*) Le nom, l'adresse, les numéros de téléphone et de télécopieur ainsi que l'adresse de courriel de l'auteur correspondant.

Noms des auteurs

Le directeur scientifique encourage tous les auteurs à fournir leur prénom au complet plutôt qu'une simple initiale.

Résumé

Chaque contribution doit être accompagnée d'un résumé qui utilisera un vocabulaire évocateur, susceptible de capter l'intérêt des lecteurs visés. Ceci est particulièrement important en vue du dépouillement automatisé que font les services de repérage de l'information de même que les robots des moteurs de recherche. Un résumé comptera au plus 175 mots et sera présenté sur une page distincte. Le résumé concis doit refléter précisément le contenu du manuscrit et doit compléter le titre plutôt que simplement le reprendre. Les résumés sont traduits en anglais ou en français, selon le cas, par les traducteurs du Journal. En revanche, les auteurs qui peuvent soumettre leur résumé en français et en anglais sont invités à le faire. Le résumé ne devrait pas contenir de références à moins que cela ne soit essentiel. Dans ce dernier cas, il faudra fournir l'information bibliographique intégrale.

À l'instar du titre, le résumé permet au lecteur de prendre connaissance du contenu du manuscrit et de décider si, oui ou non, il lui faut le lire en entier. Les auteurs devraient présenter, au début du résumé, la principale conclusion de l'étude et l'appuyer par les résultats pertinents. Ils ne doivent donner que les détails des méthodes nécessaires à la compréhension de la démarche et les intégrer à l'énoncé des résultats. Il faut éviter l'emploi de phrases telles que « ... on y analyse » ou « ... a été trouvé » et être plus spécifique. Comme le résumé est souvent séparé du corps principal de l'article par les services d'analyse et les indexateurs et qu'il s'agit parfois de la seule partie de l'article que certains lecteurs auront l'occasion de voir, il importe qu'il reflète précisément le contenu du manuscrit et qu'il soit complet en lui-même, c.-à-d. qu'il contienne seulement des références absolument *essentielles* et facilement retraçables (p. ex. R.B. Deriso. 1980. Can. J. Fish. Aquat. Sci. **37** : 268–282).

Introduction

Les auteurs doivent limiter l'introduction à la portée, au but et à la raison de l'étude. Ils ne mentionneront que les travaux publiés et autres documents nécessaires à la définition du problème et du contexte. Les auteurs devraient tout d'abord décrire le but ou la portée de l'étude, définir ensuite le problème puis présenter des repères qui orienteront le lecteur. En général, une introduction comprendra de 375 à 500 mots.

Matériel et méthodes

La section « Matériel et méthodes » jette les fondations de la résolution du problème posé dans l'énoncé du travail.

Les auteurs limiteront les renseignements sur le matériel et les méthodes à ce qui est nécessaire pour juger de la validité des résultats. Cette évaluation sera facilitée si toute l'information connexe est présentée, autant que possible, dans une même section. S'il s'agit d'outillage ou de techniques connus, les auteurs incluront des références aux publications et ne décriront en détail que les adaptations. Il y a souvent avantage à commencer un énoncé des méthodes par une phrase qui en indique le but, comme : « Afin de déterminer ... nous ... ». Si la section est longue, les auteurs devraient la diviser à l'aide d'en-têtes correspondant aux en-têtes de la section des résultats.

Résultats

Les auteurs doivent limiter les résultats aux réponses apportées aux questions en rapport avec l'énoncé de travail et faire en sorte que ces réponses soient aussi complètes que possible tout en étant concises. Les résultats doivent être associés aussi étroitement que possible aux observations ou aux mesures, ceci afin que le lecteur ne confonde pas constations et spéculations. Les auteurs devraient dégager les principales constations mises en évidence par les tableaux et les illustrations et éviter de répéter dans le texte ce que les légendes expriment clairement. La documentation complémentaire au texte peut faire partie de la documentation du rapport intégral ou être versée dans un dépôt de données reconnu. Les auteurs peuvent y faire référence dans le texte (cf. section « Données supplémentaires »).

Discussion

Les auteurs devraient limiter la discussion à la présentation des principales contributions de l'étude et à l'interprétation de constatations particulières, en les comparant avec celles d'autres auteurs. Ils mettront l'accent sur la synthèse, l'interprétation et la présentation de généralisations et de principes largement applicables. S'il existe des exceptions ou des aspects douteux, les auteurs le souligneront et feront ressortir la manière dont les résultats corroborent ou contredisent les travaux déjà publiés. La spéculation doit se limiter à ce qui peut être appuyé sur des preuves raisonnables. Les auteurs devraient terminer cette section par un sommaire de l'importance du travail et par les conclusions qu'il a invitées. Si la discussion est brève et précise, elle peut être combinée avec les résultats en une seule section.

Remerciements

Les remerciements sont rédigés à la troisième personne. Les auteurs sont priés de limiter les remerciements aux personnes qui ont étroitement contribué aux aspects scientifiques et techniques de l'article, qui ont fourni une aide financière ou

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qui ont sensiblement amélioré la qualité de la présentation. Les remerciements ne devraient pas viser les fournisseurs de service de soutien.

Notes infrapaginales

Les notes infrapaginales ne devraient figurer dans le corps du texte que lorsqu'elles sont indispensables; toutefois, leur utilisation dans les tableaux est encouragée. Lorsque des notes infrapaginales figurent dans le texte, les appels devraient être signalés à l'aide d'un chiffre arabe en exposant (sauf dans le cas des tableaux, cf. ci-dessous) et numérotés de façon consécutive à partir de la première note infrapaginale, y compris toute note apparaissant en page titre. Chaque note infrapaginale doit figurer au bas de la page où elle est signalée, **pas dans la bibliographie.**

Équations et liste de symboles

Les **équations** doivent être clairement dactylographiées et, si elles incluent des exposants ou des indices, être dactylographiées à triple interligne. Les exposants et les indices doivent être lisibles et correctement placés. Il convient de rendre évidente la distinction entre la lettre *l* et le chiffre *un*, et entre la lettre majuscule *O* et le chiffre *zéro*. Une lettre ou un symbole ne devrait être associé qu'à une seule réalité et devrait être utilisé de façon uniforme dans l'article. Chaque variable doit être définie dans le texte ou dans une **liste des symboles** qui succédera à la bibliographie. Les variables représentant des vecteurs, des matrices, des matrices vectorielles et des tenseurs doivent être clairement définies. Les équations doivent être identifiées à l'aide de chiffres arabes placés entre parenthèses, alignés avec la **marge de gauche**. Aucune distinction n'est faite entre la numérotation des formules mathématiques et celle des formules chimiques.

Références

Présentation générale

Il appartient aux auteurs d'assurer l'adéquation entre le contenu des références bibliographiques et l'information bibliographique des publications citées. Dans le texte, les références doivent être signalées à l'aide du nom des auteurs et de l'année de publication, p. ex. (Martial 1970) ou Dupont et Tremblay (1990), selon la structure de la phrase. Lorsqu'il y a trois auteurs ou plus, le nom du premier auteur est suivi de la mention et al. (p. ex. Dupont et al. 1991). Lorsque le nom et l'année ne suffisent pas à distinguer deux ouvrages, les lettres *a*, *b*, *c*, etc. sont ajoutées après l'année (à la fois dans le texte et dans la bibliographie), p. ex. Dupont 1983*a*, 1983*b*; Dupont et al. 1980*a*, 1980*b*).

Les adresses Web (adresses URL) ou les identificateurs d'objets numériques (système DOI) permettent de consulter les références qui sont accessibles sur le Web. Les auteurs sont invités à les utiliser et à les inclure avec les références dans la bibliographie (voir exemple ci-dessous).

Rapports non publiés, communications personnelles et documents sous presse

Les références bibliographiques à des rapports non publiés, à des communications personnelles ou à des articles en cours d'examen ne paraîtront pas dans la bibliographie. Elles seront plutôt signalées entre parenthèses dans le texte. Elles devront contenir le nom des auteurs et leur initiales. Dans le cas des communications personnelles, il convient de préciser la nature de la source et l'année (p. ex. J.S. Ernst (communication personnelle, 1999)). Si l'on doit citer des rapports d'experts-conseils ou d'autres documents dont la distribution est limitée, on devra préciser l'endroit où l'on peut se les procurer. Si un livre ou un article non publié avéré est **en attente de publication**, sa référence doit apparaître dans la bibliographie et porter la mention « sous presse ». Dans ce cas, il ne faut pas préciser le volume et le numéro de la page, puisque cette information risque de changer lors du processus de publication.

Présentation de la bibliographie

Dans la **bibliographie**, qui apparaît à la suite du texte, les références sont composées à double interligne et classées par ordre alphabétique du nom du premier auteur, sans numérotation. Si la bibliographie comprend plusieurs publications d'un même premier auteur, les règles suivantes s'appliquent : (*i*) les articles avec **un seul auteur** sont signalés en premier, par ordre chronologique, en commençant par le plus ancien; (*ii*) viennent ensuite les articles avec **deux auteurs**, en ordre alphabétique du nom de famille du second auteur; (*iii*) puis viennent les articles de **trois auteurs et plus**, en ordre chronologique.

Directives générales quant aux références

On choisira les références avec soin, les limitant aux publications importantes. Les références doivent refléter le style des numéros récents du Journal. Le titre d'une revue doit être abrégé conformément au *Chemical Abstracts Service Source Index* (*CASSI*) (Chemical Abstracts Service, 2540?Olentangy River Road, P.O. Box 3012, Columbus, OH 43210-0012, É.-U.). En cas de doute, les auteurs doivent écrire le nom de la revue au complet. Nous recommandons aux auteurs de préciser le numéro des revues citées et de l'indiquer entre parenthèses après le numéro du volume. La liste de références qui suit reflète les normes de ponctuation, de présentation et d'abréviation préconisées.

Exemples de divers types de références, y compris les références à des documents électroniques

Article de revue comprenant un système DOI :

Newbury, M.G., et Ashworth, A.C. 2004. A fossil record of colonization and response of lacustrine fish populations to climate change. Can. J. Fish. Aquat. Sci. **61**(10): 1807–1816. doi:10.1139/F04-113.

Article de revue comprenant une adresse Web :

Newbury, M.G., et Ashworth, A.C. 2004. A fossil record of colonization and response of lacustrine fish populations to climate change. Can. J. Fish. Aquat. Sci. **61**(10): 1807–1816. Disponible à pubs.nrc-cnrc.gc.ca/cgi-bin/rp/rp2_abst_f?cjfas_f04-113_61_ns_nf [cité 28 October 2005].

Article de revue disponible en ligne seulement (identificateur DOI) :

van der Sanden, J.J., et Hoekman, D.H. 2005. Review of relationships between grey-tone co-occurrence, semivariance, and autocorrelation based image texture analysis approaches [en ligne]. Can. J. Remote Sens. **31**(3): 207–213. doi:10.1139/rs03-011.

Numéro intégral d'une revue :

Gordon, D.C., Jr., et Hourston, A.S. (*Directeurs de la rédaction*). 1983. Proceedings of the Symposium on the Dyna-

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mics of Turbid Coastal Environments. Can. J. Fish. Aquat. Sci. **40** (Suppl. 1).

Rapport :

Pigeon, M., et Langlois, M. 1987. Étude de la durabilité au gel d'un ciment avec fumée de silice. Ciments Saint-Laurent, Beauport (Québec). Rapp. GCT-87-09.

Livre :

Lacroix, P., et Lalonde, J. (*Directeurs de la rédaction*). 1992. Les grands barrages. Éditions Poly-Sciences, Montréal (Québec).

Livre faisant partie d'une collection :

Scott, W.B., et Crossman, E.J. 1973. Freshwater fishes of Canada. Bull. Fish. Res. Board Can. n° 184.

Section d'un livre :

Healey, M.C. 1980. The ecology of juvenile salmon in Georgia Strait, British Columbia. *Dans* Salmonid ecosystems of the North Pacific. *Sous la direction de* W.J. McNeil et D.C. Himsworth. Oregon State University Press, Corvallis (Oregon). p. 203–229.

Article d'un compte rendu de conférence :

Kemp, A.L.W. 1969. Organic matter in the sediments of Lakes Ontario and Erie. *Dans* Proceedings of the 12th Conference on Great Lakes Research, Ann Arbor (Michigan), du 5 au 7 mai 1969. Association internationale de recherche sur les Grands Lacs, Ann Arbor (Michigan). p. 237–249.

Publication ou brochure d'institution :

Dzikowski, P.A., Kirby, G., Read, G., et Richards, W.G. 1984. The climate for agriculture in Atlantic Canada. Disponible auprès du Atlantic Advisory Committee on Agrometeorology, Halifax (Nouvelle-Écosse). Publ. ACA 84-2-500. n° Agdex 070.

Auteur collectif :

American Public Health Association, American Water Works Association et Water Pollution Control Federation. 1975. Standard methods for the examination of water and wastewater. 14e éd. American Public Health Association, American Water Works Association et Water Pollution Control Federation, Washington (District de Columbia).

Mémoire :

Keller, C.P. 1987. The role of polysaccharidases in acid wall loosening of epidermal tissue from young *Phaseolus vulgaris* L. hypocotyls. Mémoire de maîtrise ès sciences, Département de botanique, The University of British Columbia, Vancouver (Colombie-Britannique).

Document sur un site Web :

Quinion, M.B. 1996. Citing online sources: advice on online citation formats [en ligne]. Disponible à worldwidewords.org/articles/citation.htm [cité le 20 octobre 2005].

Traduction :

Koike, A., et Ogura, B. 1977. Selectivity of meshes and entrances of shrimp traps and crab traps. J. Tokyo Univ. Fish. **64**: 1–11. [Traduit du japonais par Can. Transl. Fish. Aquat. Sci. 4950, 1983.]

Tableaux

Les tableaux, qui occuperont chacun une page distincte, doivent suivre la bibliographie, être numérotés de façon continue en chiffres arabes dans l'ordre de mention dans le manuscrit et comporter un bref titre descriptif, d'au plus une phrase, intelligible sans qu'il ne soit nécessaire de se reporter au texte. Les titres de colonne doivent être brefs, mais peuvent être étoffés à l'aide de notes infratabulaires. Les tableaux ne doivent pas contenir de traits verticaux. Les auteurs voudront consulter un exemplaire du Journal pour s'enquérir de la présentation souhaitable des tableaux. Les notes infratabulaires doivent être signalées par des symboles (selon l'ordre suivant : *, †, ‡, §, ||, ¶, #) ou des lettres minuscules en italique placées en exposant. Une note descriptive qui n'est pas introduite par un appel de note peut être inscrite au bas du tableau à titre de **Nota**. Les auteurs éviteront d'insérer de nombreux petits tableaux et garderont le nombre de tableaux au minimum.

Légendes des illustrations

Les légendes des illustrations doivent constituer une liste **sur une page distincte**, qui suivra les tableaux. Les légendes devraient être descriptives de sorte qu'il ne soit pas nécessaire de se reporter au texte. Elles ne devraient pas inclure d'information expérimentale : celle-ci aura plutôt été présentée comme il se doit dans la section « Méthodes ». Dans les graphiques, les légendes ne doivent pas reprendre le label des axes mais plutôt décrire ce que révèlent les données. Dans le cas de montages d'illustrations, les auteurs rédigeront une légende globale contenant suffisamment d'information pour décrire l'ensemble du montage. Si chaque élément mérite sa propre légende, le montage sera fractionné et les illustrations seront plutôt présentées de façon individuelle.

Annexes

Une annexe est un document distinct et complet. Les illustrations et les tableaux présentés dans les annexes doivent être numérotés de façon consécutive, distinctement des illustrations et tableaux du corps de l'article, p. ex. figure A1, tableau A1, etc. Si les annexes contiennent des références bibliographiques, ces dernières doivent apparaître dans une bibliographie distincte de la biographie du corps de l'article. S'il y a plus qu'une annexe, veuillez les identifier de la façon suivante : Annexe A, Annexe B, etc.

Données supplémentaires

Les données supplémentaires comprennent des tableaux, des figures (cartes), des calculs détaillés et des ensembles de données produits par les auteurs dans le cadre de leur recherche, mais qui ne sont pas essentiels à la compréhension ni à l'évaluation de l'article, et qui ne seront pas publiés dans la version imprimée du Journal. Selon la politique du Journal, les données de ce genre peuvent ou non être évaluées par les pairs. Les données supplémentaires doivent être soumises avec l'article. Pour la soumission en direct (**OSPR**EY), joindre les fichiers concernés à la rubrique « Données supplémentaires ». Le Conseil national de recherches du Canada administre un dépôt des données non publiées dans lequel les données supplémentaires peuvent être versées, à la demande des auteurs ou du directeur scientifique. De plus, il est possible d'accéder gratuitement à ces données dans leur format d'origine à partir du site Web du Journal, grâce aux hyperliens à cet effet apparaissant dans la version Web de l'article. Les tableaux et les illustrations doivent être numérotés

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de façon consécutive, distinctement de ceux destinés à la publication (p. ex. figure S1, tableau S1). Chaque ensemble de données supplémentaires doit faire l'objet d'une note infrapaginale dans l'article imprimé. Des exemplaires imprimés des données déposées peuvent être obtenus contre paiement auprès du Centre de dépôt de données non publiées, ICIST, Conseil national de recherches Canada, Ottawa, ON K1A 0R6, Canada.

Programmes informatiques

La Rédaction ne publie habituellement pas les imprimés détaillés produits à l'aide de programmes informatiques. Si les données contenues dans un tel imprimé contribuent sensiblement à la valeur de l'article, l'auteur doit soumettre par voie électronique l'information relative au programme à titre de données supplémentaires (cf. section ci-dessus).

Illustrations

Généralités

Chaque illustration ou groupe d'illustrations doit être préparé de manière à occuper, après réduction, l'espace d'une ou deux colonnes du texte. Les dimensions définitives maximales d'une illustration sur une colonne sont de 8,6 sur 23,7 cm (3,4 sur 9,3 po) et celles d'une illustration sur deux colonnes de 18,2 sur 23,7 cm (7,2 sur 9,3 po). Les illustrations (y compris les similis) sont numérotées en chiffres arabes de façon consécutive. Elles doivent toutes être signalées dans l'article et être intelligibles sans qu'il ne soit nécessaire de se reporter au texte. Tous les termes, les abréviations et les symboles qu'elles contiennent doivent être identiques à ceux qui apparaissent dans le texte. Seuls les détails essentiels devraient être identifiés; l'information détaillée devrait figurer dans la légende. Les auteurs sont priés de ne pas soumettre de photographies en ton non continu (tramées) ni d'illustrations balayées puis imprimées au laser. En effet, la reproduction de ces documents cause souvent des moirures, c.-à-d. un effet visuel indésirable résultant du rebalayage ou du retramage d'une illustration formée de points.

Dessins au trait

L'épaisseur des traits doit être suffisante (au moins 0,5 point) pour que la reproduction soit nette; tous les symboles, les exposants, les indices et les signes décimaux doivent être proportionnés au reste du dessin et d'une dimension suffisante pour permettre la réduction nécessaire sans perte de détail. Il convient de ne pas utiliser de petits symboles ouverts, qui ont tendance à se refermer lorsqu'ils sont reproduits. **Les caractères d'imprimante à points, de machine à écrire ou écrits à la main ne sont pas acceptables.** Les illustrations de dimensions semblables doivent afficher le même style de police et la même dimension de caractère. Les imprimés originaux des **spectromètres RMN, IR, RPE,** etc. ne sont pas acceptables. Ils doivent être retracés au propre.

Cartes

Les cartes doivent avoir des **motifs clairs et gras**, et comporter les longitudes et latitudes (ou les coordonnées de Mercator transverses universelles) de même qu'une échelle graphique, ceci afin de pouvoir repérer avec exactitude l'emplacement du travail. Sur **les cartes du Québec**, le nom officiel des municipalités doit être utilisé (p. ex. Québec, Montréal, Clarke City). De plus, le nom des éléments topographiques doit systématiquement être en français (p. ex. Lac Bienville), à l'exception des noms d'intérêt pancanadien. En effet, ces noms ont une version officielle française et anglaise (p. ex. « Océan Atlantique » et « Atlantic Ocean ») et doivent donc être présentés dans la langue de l'article. La province de Québec, dans les cartes en anglais, doit être désignée « Quebec ». Les auteurs trouveront une liste complète des noms des régions d'intérêt pancanadien dans *Le guide du rédacteur* (p. 236–237, 2e édition, 1996), publié par Travaux publics et Services gouvernementaux Canada, Ottawa, ON K1A 0S5.

Photographies

Les photographies doivent être en ton continu, de première qualité, avec contrastes bien marqués, rognées de façon à ne laisser paraître que les éléments essentiels. Une photographie ou un groupe de photographies doit être préparé de manière à occuper, **sans réduction supplémentaire**, une ou deux colonnes du texte. Les micrographies électroniques et les photomicrographies doivent comporter une échelle graphique à même le cliché. Pour assurer un bon résultat de la reproduction, les auteurs uniformiseront le contraste et la densité de toutes les photographies montées sur une même planche.

Illustrations en couleur

Les illustrations en couleur sont reproduites aux frais de l'auteur. Les auteurs qui désirent en savoir davantage doivent communiquer avec la rédactrice administrative du Journal, Cecily Pearson (613-993-9099; télécopieur : 613-952-7656; courriel : cecily.pearson@nrc-cnrc.gc.ca).

Préparation des fichiers graphiques électroniques

Le logiciel graphique que préconisent les Presses scientifiques du CNRC est CorelDraw! Pour connaître les applications compatibles, les auteurs peuvent se reporter à la liste des programmes graphiques électroniques à pubs.nrc-cnrc.gc.ca/fra/revues/graphiques.html.

Les versions PC ou Macintosh des polices True Type ou Type 1 doivent être utilisées. **Les auteurs ne doivent pas se servir des polices de caractères en mode point ou non standard**.

Toutes les illustrations doivent être soumises dans leur dimension de tirage final. Quant aux illustrations comportant plusieurs parties (p. ex., *a*, *b*, *c*, *d*, etc.) crées sur le même logiciel, elles doivent être regroupées dans un seul fichier plutôt que transmises individuellement.

Il convient de garder les illustrations le plus simple possible afin d'éviter les complications. Les auteurs voudront éviter les textures et les fonds grisés compliqués, particulièrement dans les programmes d'illustration vectorielle, puisque ceci risque d'altérer la qualité des illustrations au moment du tirage.

Les **fichiers d'images en mode point** sont produits selon une grille dans laquelle chaque carré (ou pixel) correspond à une nuance de noir, de couleur ou de gris. Un fichier en mode point (ou de données tramées) est défini par le nombre de pixels ou d'éléments d'image par pouce. Comme le pixel est défini comme un point, on parle aussi de « points par pouce » ou « ppp ». Plus la résolution de l'image est élevée, plus le nombre de points sur une surface donnée est élevé. Les illustrations soumises en mode point doivent être de réso-

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lution suffisante. Les exigences minimales de résolution sont les suivantes : 600 ppp pour les dessins au trait, 1200 ppp pour les traits fins (les dessins au trait comportant des traits fins ou un fond grisé), 300 ppp pour les similis et les couleurs et 600 ppp pour les combinaisons (similis avec caractères à l'extérieur de l'espace réservé à la photo).

Tous les **fichiers en couleur** soumis doivent être en mode couleur CMJN (cyan, magenta, jaune et noir). Ces couleurs sont utilisées pour l'impression commerciale en polychromie. Les graphiques RVB (rouge, vert et bleu), soit le mode couleur pour la production d'images à l'écran, ne s'impriment pas correctement.

Les **fichiers vectoriels** sont des fichiers d'images composées d'éléments tels que des traits et des formes. Ce type de fichier est habituellement utilisé pour les dessins au trait.

Les éléments en mode point peuvent être importés dans un logiciel vectoriel ou de dessin pour ajouter ou superposer de l'information, des traits, du texte, etc. Les éléments d'image en mode point ne doivent pas être redimensionnés, recadrés, tournés ou manipulés de quelque façon après avoir été importés.

Formats multimédias — Il est maintenant possible d'inclure des extraits audio et vidéo dans les textes intégraux des revues des Presses scientifiques du CNRC publiées en HTML. Les principaux formats multimédias sont acceptés. Pour plus de détails, consultez la liste des fichiers acceptés dans le site Web du Journal.

Directives pour les manuscrits

Guides de style

Il est recommandé d'utiliser, comme guide général dans le domaine de la biologie, *The CSE Manual for Authors, Editors, and Publishers : Scientific Style and Format* (7e édition, 2006), publié par le Council of Science Editors (Reston, VA 20190, É.-U.).

Orthographe

L'orthographe doit respecter celle du *Petit Robert*. Les auteurs sont responsables de l'uniformité de l'orthographe dans l'ensemble du texte. Les accents doivent être insérés sur les majuscules.

Nomenclature, abréviations et acronymes

La nomenclature et les abréviations doivent être conformes aux règles proposées par la Commission des rédacteurs de revues de biochimie de l'Union internationale de biochimie (UIB) en collaboration avec l'UICPA. Il est recommandé d'utiliser, comme guide général dans le domaine de la biologie, *The CSE Manual for Authors, Editors, and Publishers : Scientific Style and Format* (7e édition, 2006), publié par le Council of Biology Editors (Reston, VA 20190, É.-U.). En matière de nomenclature des enzymes, il convient de consulter la publication *Enzymes nomenclature (1992): Recommendations of the Nomenclature Committee of the International Union of Biochemistry and Molecular Biology* (Academic Press, San Diego (Californie)).

Il n'est pas nécessaire de définir les abréviations et les acronymes d'usage courant dans le domaine. Toutes les autres doivent être définis à la première mention dans le texte et ceux ayant plus d'une signification ne devraient pas être utilisés.

Unités de mesure

Il est recommandé de se servir du **Système international d'unités** ou, à tout le moins, de fournir les équivalences en unités SI. Éviter les formes ambiguës, telles que g C/m^2/jour; utiliser plutôt g C·m^{-2}·jour^{-1}. Ce système est décrit dans le *Guide de familiarisation au système métrique*, CAN/CSA-Z234.1-00, publié par l'Association canadienne de normalisation (178, boulevard Rexdale, Toronto, ON M9W 1R3, Canada). Pour des raisons pratiques, la Rédaction admet parfois certaines exceptions à l'utilisation du Système international d'unités.

Analyses statistiques

Les hypothèses ou le modèle sous-jacent à toute analyse statistique doit être clairement énoncé. Les symboles * et ** , indiquant les niveaux de signification, ne doivent être utilisés que s'ils sont accompagnés des valeurs réelles de la valeur à tester. Il est préférable d'utiliser les valeurs réelles de *p*.

Poissons

Pour le nom des poissons et leur orthographe, le Journal adhère aux recommandations contenues dans *Common and Scientific Names of Fishes from the United States, Canada, and Mexico* (6e éd., Spec. Publ. No. 29, American Fisheries Society, 2004). Pour la nomenclature génétique pour les loci de codage des protéines, le Journal adhère aux recommandations contenues dans Shaklee et al. (Trans. Am. Fish. Soc. **119** : 2–15, 1990).

Nombres

Les nombres de cinq chiffres ou plus sont répartis en groupes de trois à partir du signe décimal, à gauche comme à droite, puis séparés par un espace (pas un point, ni une virgule ou autre symbole); on aura ainsi 23 562 987 et non pas 23,562,987. En français, le signe décimal est la virgule (p. ex. 0,1 mL) et il est précédé d'un zéro pour les nombres entre 1 et –1, sauf pour le zéro. Le symbole × indique la multiplication (p. ex. 3×10^6 et non pas $3 \cdot 10^6$).

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K.E. Bennett, J.J. Gibson, and P.M. McEachern	**83–99**	Water-yield estimates for critical loadings assessment: comparisons of gauging methods versus an isotopic approach
C.J. Watras and K.A. Morrison	**100–116**	The response of two remote, temperate lakes to changes in atmospheric mercury deposition, sulfate, and the water cycle
Etienne Rivot, Etienne Prévost, Anne Cuzol, Jean-Luc Baglinière, and Eric Parent	**117–133**	Hierarchical Bayesian modelling with habitat and time covariates for estimating riverine fish population size by successive removal method

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Volume 65, numéro 1, janvier 2008

	iii–iv	Announcement / Communiqué
Donald A. Jackson	v–vi	Editorial / Éditorial
	TRIBUTE	HOMMAGE
Jeffrey A. Hutchings	vii–xii	Ransom Aldrich Myers (1952–2007): In memoriam
Jeffrey A. Hutchings	xiii–xix	Ransom Aldrich Myers (1952–2007): In memoriam
	ARTICLES	ARTICLES
W. Gary Sprules	1–9	Ecological change in Great Lakes communities — a matter of perspective
Katja Anttila, Matti Järvilehto, and Satu Mänttäri	10–16	Ca^{2+} handling and oxidative capacity are greatly impaired in swimming muscles of hatchery-reared versus wild Atlantic salmon (*Salmo salar*)
R. Glenn Szerlong and David E. Rundio	17–26	A statistical modeling method for estimating mortality and abundance of spawning salmon from a time series of counts
Darren M. Gillis, Adriaan D. Rijnsdorp, and Jan Jaap Poos	27–37	Behavioral inferences from the statistical distribution of commercial catch: patterns of targeting in the landings of the Dutch beam trawler fleet
Takashi Sakamaki and John S. Richardson	38–46	Retention, breakdown, and biological utilisation of deciduous tree leaves in an estuarine tidal flat of southwestern British Columbia, Canada
Alexandrine Pannard, Myriam Bormans, and Yvan Lagadeuc	47–60	Phytoplankton species turnover controlled by physical forcing at different time scales
Judith Bouchard and Daniel Boisclair	61–73	The relative importance of local, lateral, and longitudinal variables on the development of habitat quality models for a river
Javier Tovar-Ávila, Christopher Izzo, Terence I. Walker, J. Matias Braccini, and Robert W. Day	74–82	Dorsal-fin spine growth of *Heterodontus portusjacksoni*: a general model that applies to dorsal-fin spines of chondrichthyans?

Continued on inside back cover / Suite au verso

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